The Development of Visual Motion Processing in Human Infants

Thesis

The development of visual motion processing in human infants

John Wattam-Bell, BA

Date of submission: 11 May 1993
Date of award: 17 August 1993

Thesis submitted for the degree of Doctor of Philosophy, June 1993

The Open University

Abstract

The experiments of this thesis have used apparent motion in random-dot patterns to explore the development of motion processing in infants. Most of the experiments involved discrimination of a segregated pattern, in which different regions moved in different ways (eg opposite directions), from a uniform pattern containing just one kind of motion.

Maximum displacement limits (d_{max}) for discrimination of coherent from incoherent motion, and for discrimination of opposite directions of coherent motion, increased between 8 and 15 weeks. The higher threshold of adults indicated that this increase continues beyond 15 weeks.

The effect of changing the interval between displacements indicated two processes underlying the increase in direction discrimination d_{max}: a maturation of the temporal properties of motion detectors (eg improving sensitivity to high temporal frequencies), which is largely complete by about 12 weeks; and a more prolonged development of their spatial properties which dominates the change in d_{max} after 12 weeks, and may also be involved before this.

Measurements of coherence thresholds for direction discrimination showed that, in addition to the rise in d_{max} with age, there is a substantial improvement in motion sensitivity at displacements below d_{max}. Hence a uniform increase in sensitivity across all displacements is likely to be an important factor behind the development of d_{max}. However there may be additional specific improvements in sensitivity to large displacements, perhaps reflecting the emergence of low spatial frequency channels.

A series of habituation and preferential looking experiments failed to find evidence for direction discrimination before 6 weeks, though positive evidence was obtained at 6-8 weeks. The results suggest that directionality emerges at about 7 weeks of age. Interestingly, despite their success at discriminating direction in a segregated stimulus, 6-8-week-olds were insensitive to the absolute direction of uniform motion. This suggests that they have not yet learnt to combine measurements of retinal image motion with information about eye movements.

Contents

	Acknowledgements	iii
	Table of illustrations	iv
	Published work	v
1	**Introduction**	1
	Visual motion processing	1
	Low-level motion mechanisms	2
	Spatiotemporal integration of local motion signals	6
	Motion pathways in the visual system	8
	The development of visual motion processing	9
	Low velocities	10
	High velocities	11
	Directional motion mechanisms	12
	Motion cues in perception	13
	Overview	15
2	**Methods**	18
	Stimuli	18
	Procedures	21
	Forced-choice preferential looking (FPL)	21
	Habituation	23
	Adult experiments	25
	Subjects	25
3	**Discrimination of coherent from incoherent motion**	26
	Pilot experiments	27
	d_{max} for discrimination between coherent and incoherent motion	28
4	**Discrimination of motion direction**	33
	d_{max} for discrimination of opposite directions of motion	33
	The effect of contrast on d_{max}	36
	The effect of displacement interval on d_{max}	37
	Coherent/incoherent and direction discrimination compared	39
	Conclusions	43

5 The onset of directionality 45
The development of d_{min} for direction discrimination 45
Motion processing in one-month-olds 47
Preferential looking experiments 47
Habituation experiments 52
Conclusions 61

6 Spatiotemporal integration in motion detection 63
Temporal integration 64
Spatial integration 66
Discussion 68
Conclusions 71

7 Discussion 73
The development of d_{max} 73
The onset of directionality 76

Appendix 1: Sub-pixel positioning 81

Appendix 2: Staircase procedures 83
The bracketing staircase 83
The 2-up/1-down staircase 85
Problems with the use of staircases with infants 86

Appendix 3: The response of low-pass mechanisms to coherent and incoherent motion 92

Appendix 4: Individual data 98

References 108

Acknowledgements

I would like to thank Jan Atkinson, Ol Braddick and Ilona Roth for their enthusiastic support and encouragement throughout this work; Ol and Jan for many helpful discussions, and for their comments on this manuscript; the staff at the VDU - Shirley Anker, Clare Hughes, Francoise Matthieu, Fiona Macpherson, Sarah Rae, Hilary Stobart, Jo Tricklebank - for their invaluable help with the infant testing and administration; and last, but by no means least, all the infants and their parents whose cooperation made this research possible.

This thesis is dedicated to Anne, Richard and Duncan.

Table of illustrations

Fig 1.1	Random-dot patterns.	*page* 2
Fig 1.2	An elementary motion detector.	3
Fig 2.1	Type 1 & type 2 random-dot patterns.	20
Fig 3.1	Stimulus schematic for coherent vs incoherent motion.	26
Fig 3.2	Development of d_{max} for coherent vs incoherent motion.	29
Fig 4.1	Development of d_{max} for discrimination of opposite directions.	35
Fig 4.2	Effect of contrast on d_{max}.	36
Fig 4.3	Effect of displacement interval on d_{max}.	38
Fig 4.4	Comparison of d_{max} for direction discrimination and coherent vs incoherent motion.	40
Fig 4.5	Adult's d_{max}.	41
Fig 5.1	Stimulus for measurement of d_{min}.	46
Fig 5.2	Development of d_{min} and d_{max}.	47
Fig 5.3	1-month-old FPL individual data (1st group).	49
Fig 5.4	1-month-old FPL group data (1st group).	50
Fig 5.5	1-month-old FPL group data (2nd group).	51
Fig 5.6	Habituation stimulus (direction discrimination, test phase).	52
Fig 5.7	3-5 weeks segregated vs uniform habituation results.	55
Fig 5.8	3-5 weeks segregated vs uniform habituation results (last 5 infants).	56
Fig 5.9	6-8 weeks segregated vs uniform habituation results.	57
Fig 5.10	Absolute direction discrimination habituation results.	59
Fig 6.1	Coherence thresholds: temporal integration.	65
Fig 6.2	Coherence thresholds: spatial integration (segregated vs uniform).	67
Fig 6.3	Coherence thresholds: spatial integration (segregated vs transparent).	68
Fig 6.4	Individual infants' coherence thresholds vs age.	69
Fig 6.5	Adult sensitivity vs displacement size.	70
Fig A1.1	Sub-pixel positioning.	82
Fig A2.1	Example of the bracketing staircase.	84
Fig A2.2	Example of the 2-up/1-down staircase.	86

Fig A2.3 Psychometric functions used in staircase simulations. 89
Fig A2.4 Staircase simulation results. 89
Fig A3.1 Temporal autocorrelation functions. 93
Fig A3.2 Temporal power spectra. 95

Published work

The results presented in Chapters 3 and 4 of this thesis have been published in full (Wattam-Bell, 1992a). In addition the results of Chapters 4 and 5 have been presented at a number of conferences, and published in abstract form (Wattam-Bell, 1991b; 1992b; 1993).

1 Introduction

Everything of interest in the visual world moves, either of its own accord, or as a result the observer's own movement. Visual motion offers a rich source of information about the environment, and a correspondingly wide variety of perceptual functions that use this information have been identified. Nakayama (1985) gives a comprehensive list of these which illustrates the extent to which motion analysis can provide information about the contents and layout of the environment, and not simply about the motion of objects within it. The central importance of motion in vision is underlined by the fact that, unlike other visual dimensions such as colour, sensitivity for motion is apparently present in all visual systems; indeed for some species it is the primary, if not the only, source of visual information about the world (Horridge, 1984).

Visual motion processing

Physically, an object's motion is specified by its velocity (ie its speed and direction of motion in space[1]). An initial requirement for perception is to estimate this quantity. The most conceptually straightforward way of estimating velocity is to sample position at two points in time. This gives average velocity over the time interval, and the shorter the interval, the closer this gets to the true (instantaneous) value of velocity.

There is now overwhelming evidence that motion is a fundamental visual dimension (Nakayama, 1985), that the space/time measurement occurs in low-level motion-sensitive mechanisms early in the visual pathway, rather than as a result of independent measurements of position and time which are combined later in the perceptual process to provide motion information. Apparent motion in random-dot patterns provides one of the most compelling demonstrations of this. Figure 1.1 shows pair of random-dot patterns, in which the second pattern is constructed by displacing all the elements of the first by the same distance and in the same direction. When they are viewed side-by-side, considerable scrutiny is needed to work out the direction of the

[1]Since the motion of objects occurs in 3 dimensions, but is projected onto the two dimensions of the retina, the visual system faces the problem of recovering motion in depth. However this thesis will be exclusively concerned with motion in the fronto-parallel plane, and the third dimension will be ignored.

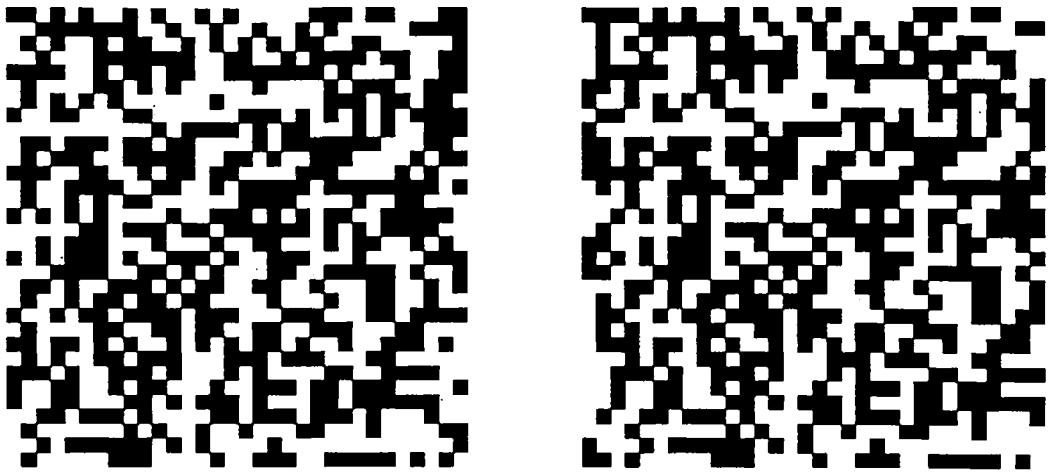

Fig 1.1 Random dot patterns. The pattern on the right is a coherently displaced version of the one on the left

displacement. However if the patterns are superimposed and viewed in quick succession, there is an immediate sense of coherent motion whose direction is clearly evident. In a by now classic experiment, Braddick (1974) demonstrated that this sense of coherent motion only occurs for small displacements over short temporal intervals, and is eliminated by presenting the patterns dichoptically. The spatial and temporal limits for random-dot apparent motion are much smaller than those reported for apparent motion with isolated figures. These findings led Braddick (1974, 1980) to suggest that random-dot apparent motion is detected by a short-range process which consists of low-level motion mechanisms early in the visual pathway (prior to the site of binocular integration), and which is distinct from the presumably higher-level long-range process underlying classical apparent motion.

Low-level motion mechanisms

The past decade has seen an increasing convergence of physiological, psychophysical and theoretical accounts of low-level motion detection. One of the earliest and most influential models was devised by Reichardt (1961) to account for data on motion processing in insects. In its crudest form, this detector samples the image at two points in the visual field (Fig 1.2). The signal from position A is subjected to a delay (ΔT) before being compared with the signal from B. The output of the comparator will be greatest for a stimulus moving in the direction AB at a speed $\Delta S/\Delta T$. Although simple,

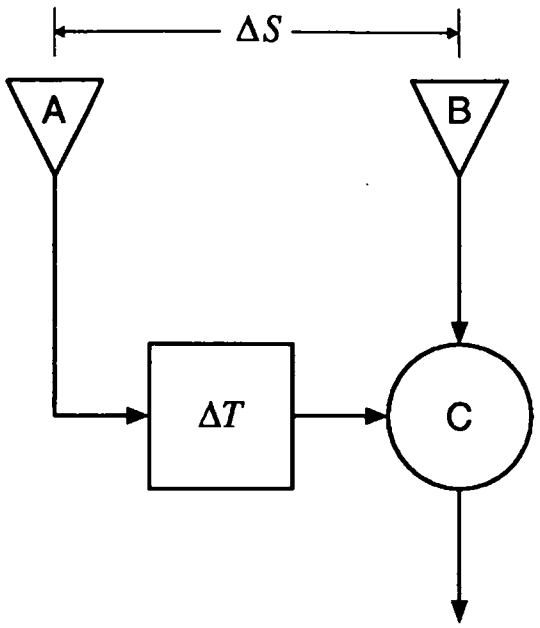

Fig 1.2 An elementary motion detector, based loosely on Reichardt's (1961) correlation model. The visual input is sampled at two positions, A and B. The signal from A is delayed (ΔT) before being compared with the signal from B by unit C. The response of C depends on the degree to which its inputs are correlated, and will be greatest when the input seen by B is a replica of A's input ΔT msec previously - ie when the visual stimulus is moving in the direction A to B at a speed of $\Delta S/\Delta T$. This detector responds best to motion in a particular direction (given by the relative positions of A and B) at a particular speed ($\Delta S/\Delta T$). In its simplest (and most unrealistic) form, A and B represent points in the visual field, and ΔT is a pure delay. In this case, the motion must exactly match the mechanism's parameters for C to detect any correlation. More realistically, A and B are finite spatiotemporal receptive fields with widths comparable to ΔS, and ΔT is not a pure delay but some form of temporal filter which behaves approximately as a delay. As a result, although the mechanism still shows an optimum speed and direction, it will respond to non-optimally moving stimuli; its speed and direction tuning will depend on the spatial and temporal properties of A and B

this model incorporates most of the key features found in theoretical and physiological motion detectors. Firstly, it is a local mechanism, ie it operates over a restricted region of the visual field. Secondly, it has a degree of selectivity for both the direction and speed of motion. It can be seen as signalling the extent to which the stimulus velocity matches its own preferred direction and speed. Evidently, to detect all possible velocities, each point in the visual field requires an array of these mechanisms with different preferred directions (determined by the orientation of the AB axis, and whether the A or B signal is delayed), and different preferred speeds (which can be varied by changing ΔS and/or ΔT).

It is well established that in the early stages of vision images are analysed by a range of (more or less) independent channels (Braddick, Atkinson & Campbell, 1978), each sensitive to a limited range of spatial frequencies (or spatial scales), temporal frequencies, and orientations, which between them cover the visible region of the spatiotemporal frequency plane. Neurons in the visual cortex show qualitatively and quantitatively similar stimulus selectivity (Hubel & Wiesel, 1959; De Valois et al, 1982a,b), which has led to a loose identification of (psychophysical) channels and (cortical) receptive fields. The spatial channels are quite narrowly tuned, so that several are needed to cover the visible range (see Wilson et al, 1990). Temporal tuning is broader, and most of the evidence suggests that there are only 2 or perhaps 3 distinct channels (Watson & Robson, 1981; Anderson & Burr, 1985)[2]. Recent developments in the modelling of motion detection have centred on incorporating it into this framework (Watson & Ahumada, 1985; Adelson & Bergen, 1985; van Santen & Sperling, 1985). The key to understanding motion in terms of spatial and temporal frequency is the well-known relationship speed = *tf/sf*. It tells us that any spatiotemporally selective mechanism (ie any visual mechanism!) will show some kind of selectivity for speed (ie the scalar part of velocity). However, to make full use of visual motion, it is also necessary to extract information about direction. This requirement naturally focuses attention on the prominent subset of visual cortical neurons which show directional selectivity; these cells are prime candidates for cortical motion detectors, and a major aim of current models has been to emulate the combination of directional and spatiotemporal frequency selectivity which is characteristic of these neurons (De Valois et al, 1982a,b), and of human motion detectors (Anderson & Burr, 1985; Burr et al, 1986).

The emphasis on directionality as the hallmark of motion sensitivity glosses over the fact that, at least in principle, non-directional spatiotemporally tuned mechanisms are adequate for many of the perceptual uses of motion analysis. Examples include speed discrimination and segregation of objects based on differences in speed (with or without differences in direction); discrimination and segregation of coherent and incoherent motion, which will be touched upon in the experiments described here; and

[2]An alternative is that there are more, but that their tuning curves overlap so much that that they cannot be easily distinguished (Lehky, 1985).

"motion deblurring" (Burr et al, 1986). This is not to deny the fundamental importance of directional information. It is central to many uses of visual motion, such as smooth pursuit (Lisberger et al, 1987), while others, such as image segmentation, can be based on direction differences alone. Moreover, over much of the spatiotemporal frequency plane, contrast thresholds for detection and for direction discrimination coincide (Watson et al, 1980) - ie the most sensitive mechanisms are directional (though this is not the case at low velocities). On the whole a strong emphasis on directional selectivity seems justified, but it would be unwise to ignore the possible involvement of non-directional mechanisms in motion analysis; even if they are of secondary importance in adults, it cannot be assumed that this is also true for infants.

The spatiotemporal frequency and space/time frameworks offer complementary accounts of motion detection, each useful in its own way. Despite the extra complexity of spatiotemporally tuned motion models, to a first approximation they too can be described in terms of a characteristic span and delay, although unlike the simple model of Fig 1.2 these parameters will exhibit appreciable tuning width about optimum values which are not necessarily entirely independent of each other; as a result, velocity tuning may not be independent of the stimulus configuration. The complementary nature of the two domains implies an approximately inverse relationship between a detector's optimum spatial frequency and its optimum ΔS; tuning for low spatial frequencies, and large values of ΔS are both associated with sensitivity to high velocities. Most models assume this is a fixed relationship (typically ΔS is equal to a quarter cycle of the optimum spatial frequency [eg Adelson & Bergen, 1985]), but this is not a necessary feature of real motion detectors, though there is some neurophysiological evidence for it (Baker & Cynader, 1986). A similar argument applies to the temporal parameters, with in general an inverse relationship between ΔT and optimum temporal frequency, though again these parameters are not necessarily rigidly linked.

The model of Fig 1.2 (ie the space/time domain version) offers a straightforward account for the spatiotemporal limits of random-dot apparent motion. It will only respond strongly to stimulus displacements close to its optimal ΔS, which leads to a simple interpretation of d_{max} (the maximum displacement for coherent apparent motion in random dots) as a measure of the largest values of ΔS in the population of motion detectors. Likewise the temporal constraints on apparent motion can be interpreted in

terms of ΔT (Baker & Braddick, 1982). This kind of analysis has been used extensively by van Doorn & Koendrink (1982a,b; van de Grind et al, 1983; 1986) to examine the variation of ΔS and ΔT with stimulus velocity and visual field location.

However a full understanding of random-dot apparent motion is not so straightforward. Braddick's (1974) original value of 15 min arc for d_{max} has since been shown to be highly dependent on a number of stimulus parameters, in ways which suggest that motion perception depends as much on the interactions between motion detectors as on the intrinsic properties of the detectors themselves. In general, the presence of motion mechanisms with appropriate values of ΔS & ΔT should be seen as a necessary, but not sufficient condition for seeing coherent motion in any particular stimulus[3].

Spatiotemporal integration of local motion signals

The signal from an individual motion detector is inherently ambiguous. Part of this ambiguity arises from the inevitably finite width of a detector's speed and direction tuning, which allows it to respond to a stimulus moving with a non-optimal velocity (since in general a detector's output will also depend on stimulus contrast, it is possible for a high contrast non-optimally moving stimulus to produce the same response as a low contrast optimally moving one). The solution is to examine the responses of a set of detectors with a range of preferred speeds and directions; velocity can be estimated from the biggest response, or more generally by interpolation. This is still a local process, involving only detectors at a single position in the visual field. However, there are other forms of ambiguity which are not so easily resolved by local measurements. One such is illustrated by the rdps of Fig 1.1. The difficulty here is deciding which of the dots in pattern (b) is the displaced partner of a given dot in (a). This problem (the correspondence problem) is also faced in motion analysis, where there is ample opportunity for a local measurement like the one described above to report motion in the wrong direction. The ambiguity here is intrinsic to the stimulus; a step-like displacement of a rdp produces motion "noise", with energy moving in all directions. However the most dominant direction will be the true one, and over the whole pattern

[3]The involvement of the long-range (Braddick, 1980) and 2nd order (Chubb & Sperling, 1988) processes in motion detection is ignored here.

the majority of the local motion "votes" will be for the true direction. Hence one way to resolve this ambiguity is by spatial integration of local motion signals, and there is good evidence that this occurs in the visual system (Baker & Braddick 1982; van Doorn & Koendrink, 1983; Williams & Sekuler, 1984). There is also evidence that it is not a simple and inflexible averaging process. For example, it must also allow motion contrast, which can result in clear segregation of differently-moving regions, with a sharp border between them; evidently spatial integration must come to an abrupt halt at such borders. A number of recent experiments suggest that the integration of motion signals, both locally and across space, occurs in a cooperative network, with mutual facilitation between detectors with similar preferred directions, and inhibition between those tuned to different directions (Chang & Julesz, 1984; Williams et al, 1986; Snowden, 1989; Snowden & Braddick, 1989; Nawrot & Sekuler, 1990).

Random dot patterns contain a wide range of spatial frequencies. Abrupt displacements divide the spatial frequency spectrum in two, at a point which depends on displacement size. Most of the energy of the spatial frequency components below this point signals the true direction of motion, whereas above it, motion noise predominates. Hence one way to improve motion detection would be to isolate the low frequency components, ie to use motion mechanisms tuned to low spatial frequencies; since low spatial frequency mechanisms have large receptive fields, this is a form of spatial integration, but one that occurs before, or at least simultaneously with, motion detection. Such mechanisms undoubtedly exist in the visual system (Anderson & Burr, 1987), and given that a motion detector's span (and thus the largest displacement that it can detect) is inversely related to it optimum spatial frequency, one might expect d_{max} for random-dot apparent motion to depend on these low spatial frequency mechanisms. However, low-pass spatial filtering of a random-dot pattern produces a large increase in d_{max} over that found with the original, unfiltered pattern (Chang & Julesz, 1983b; Cleary & Braddick, 1990b). The information carried by low spatial frequencies is present in both the filtered and unfiltered patterns, but with the unfiltered pattern it is effectively masked by the noise signals from high spatial frequencies. Cleary & Brradick (1990b) have suggested that the masking results from interactions between motion detectors tuned to high and low spatial frequencies, and that d_{max} is determined by the highest frequency detector present. Alternatively, d_{max} may depend on the lowest

spatial frequency mechanism available, with the limit arising when there is a significant intrusion of noise from adjacent higher spatial frequencies into its pass-band (Eagle, 1992). Whichever is the case, it is likely that this masking is unique to apparent motion, since with continuous motion high spatial frequencies do not generate motion noise, but are simply blurred into invisibility (see Nakayama, 1985).

Temporal integration offers another means of disambiguating motion signals. For a variety of tasks, motion detection improves when stimulus duration is increased (eg van Doorn & Koendrink, 1984; McKee & Welch, 1985). Temporal recruitment results in an increased d_{max} for each of a sequence of displacements compared with that for a single isolated displacement (Nakayama & Silverman, 1984; Snowden & Braddick, 1989a,b). Snowden and Braddick provide evidence for two distinct forms of temporal recruitment; one involves the recruitment of detectors with longer spans and delays, which is made possible by the increased stimulus duration, while the other results from the kind of cooperative interactions described above, with the added assumption that the effects of these interactions persist in the network for a finite period.

Motion pathways in the visual system

The different functions of motion information in vision often involve different kinds of analysis. For example, accurate control of smooth eye movements requires precise estimation of velocity. For optokinetic nystagmus (OKN), this is presumably a global measurement of average velocity over large parts of the visual field, while smooth pursuit must depend on local measurements which extract the velocity of the pursued object from other motions in the background. On the other hand, the segregation of objects based on differences in speed and/or direction demands precise localization of discontinuities in velocity, but does not need accurate measurement of the velocities involved.

These diverse kinds of analysis suggest that at some level visual motion processing must split into functionally distinct systems, though they may of course merge again later, as for example smooth pursuit and OKN signals must do in the final common pathway for eye movements. In the primate visual system, there are at least two anatomically distinct motion pathways which diverge early on, possibly at the level of the retinal ganglion cells. The first, a subcortical projection from the retina to the

nucleus of the optic tract (NOT), appears to be exclusively involved in the generation of OKN (Hoffmann, 1986). The second pathway, the projection via LGN to striate cortex (area V1) and beyond, is presumably responsible for all other aspects of motion analysis; moreover in adults (but probably not in young infants - see below) this pathway plays a major role in the control of OKN via the cortical projection to NOT. One prominent division of the geniculostriate pathway, the magnocellular projection via V1 and V2 to area MT, appears particularly specialised for motion processing (see Maunsell & Newsome, 1987). The majority of MT neurons are directionally selective, and the variety of different responses to moving stimuli found in MT and areas further upstream such as MST suggests that a good part of the division of motion processing into different functional streams may be happening in this pathway.

The main input to MT comes directly or indirectly from layers 4B and 6 of V1. A high proportion of neurons in these layers are directionally-selective (Orban et al, 1986), which suggests they may represent the initial stage of directional motion processing which is further elaborated by MT. The comparable upper velocity cut-offs found in MT and layer 4B support this notion (Orban et al, 1986), though differences in displacement limits for apparent motion between V1 and MT (Mikami et al, 1986) suggest the picture is more complicated than this. Outside these layers the proportion of directionally-selective cells is smaller, and their velocity cut-offs tend to be lower (Orban et al, 1986), and it has been suggested that MT is particularly involved the perception of high(er) velocities, with V1 playing a more prominent role at low velocities (Newsome et al, 1986), an idea that has an interesting parallel in the psychophysical evidence for qualitative differences in motion processing at low and high velocities (Bonnet, 1982; Snowden & Braddick, 1990). MT is generally regarded as part of the "where" cortical stream (Mishkin et al, 1983); if there is a distinct slow motion pathway arising in V1 and not involving MT then it may be part of the "what" stream. This notion is quite plausible - motion cues are an important source of both "what" and "where" information (Nakayama, 1985).

The development of visual motion processing

From an evolutionary point of view, motion processing appears to be the most primitive form of visual analysis. Horridge (1984) has argued that "in evolution and in

ontogeny of visual processing, relative motion is the first cue whereby objects are distinguished at all, and the whole system of recognition of objects and their discrimination is superimposed later on the motion processing system". The evidence he produces is almost exclusively concerned with the evolutionary importance of visual motion; to date there is little evidence for (or against) its primary role in development. Nevertheless, its undoubted prominence in evolution and in adult vision does lead to the expectation that motion sensitivity will be among the earliest of visual functions to emerge during development. In fact, there are two long established observations of motion sensitivity in newborn infants. The first is that newborns' visual attention is strongly attracted by moving objects; the second is that, with appropriate stimuli, newborns show optokinetic nystagmus.

Low velocities

A preference for moving stimuli is one of the more striking aspects of infant visual behaviour. This preference extends to non-moving temporally modulated stimuli (ie flicker). In other words motion preference is not of itself evidence for true motion sensitivity; it may simply be a response to the temporal modulation which inevitably occurs with motion. Nevertheless there have been several studies which have used this preference to explore the effect of velocity on infants' discrimination of a moving stimulus from a similar stationary one, and which provide some insight into the development of motion sensitivity. Volkmann and Dobson (1976) were among the first to show that infants prefer the moving stimulus only for velocities above a relatively high minimum, and that this lower velocity threshold (v_{min}) decreases with age. A number of other studies have confirmed this trend, though with some disagreement about the actual value of v_{min} at particular ages. For example Aslin and Shea (1991), using squarewave gratings, found thresholds of around 9 deg/sec at 6 weeks, falling to 4 deg/sec at 12 weeks; moreover, these values were not significantly changed by a two-fold change in grating spatial frequency. This rules out a pure temporal frequency limit, which would result in v_{min} being proportional to 1/(spatial frequency)[4], but as the authors point out leaves open the question of whether position- or motion- sensitive

[4]This follows from the well-known relationship for drifting gratings, velocity=(temporal frequency)/(spatial frequency).

mechanisms are involved. However, there are two studies using standing wave motion (Dannemiller and Freedland, 1991, 1992; Bradbury et al 1990) which show that purely position-sensitive mechanisms cannot account for infants' discrimination of moving from static stimuli. Thus, not surprisingly, both the spatial and temporal properties of the mechanisms involved are relevant. To account for the existence of a lower velocity threshold, and its (perhaps approximate) invariance with spatial frequency (Aslin & Shea, 1991), the minimum requirement is a mechanism with bandpass temporal and lowpass spatial frequency tuning. The developmental improvements in acuity and contrast sensitivity of the infant visual system (van Sluyters et al, 1991) will increase the sensitivity of these mechanisms to low velocities, leading to the observed decrease in v_{min} with age. One property not required of these mechanisms is directional-selectivity; discrimination between moving and static stimuli does not need directional information. These experiments may not be measuring thresholds of motion mechanisms in the narrow (ie directional) sense defined above[5]. Nevertheless, these results must at least provide lower bounds for v_{min} of directional mechanisms. In addition, if directional v_{min} is also constrained by acuity and contrast sensitivity, it should show the same decrease with age.

High velocities

As for adults, measurements of infant temporal contrast sensitivity provide some information on the upper bounds of motion detection. Regal (1981) found that critical flicker frequency develops rapidly to near adult levels (around 50 Hz) by 2-3 months, in marked contrast to the much more leisurely improvement in spatial acuity (Gwiazda et al, 1980). Despite this relatively high temporal acuity, infants show poor sensitivity at lower temporal frequencies. As a result the temporal contrast sensitivity function (CSF) is quite flat and appears to be low-pass in infants younger that about 2 months (Teller et al, 1992; Hartmann & Banks, 1992). After this, the temporal CSF becomes band-pass, first at low spatial frequencies, but only later at higher spatial frequencies (Hartmann & Banks, 1992; Swanson & Birch, 1990). This may reflect the emergence of bandpass temporal mechanisms. Alternatively it may reflect changes in the spatial

[5]Though as discussed above, non-directional mechanisms can offer a degree of motion vision, and in a visual system without directional detectors this could be of considerable importance.

tuning of the underlying mechanisms without necessarily any change in temporal tuning (see Hartmann & Banks, 1992; and Swanson & Birch, 1990).

Since these studies used flickering (ie non-moving) stimuli to measure temporal sensitivity they don't provide direct information on motion sensitivity. However as Hartmann and Banks point out, infants' contrast sensitivity is most adult-like at high temporal frequencies and low spatial frequencies. They should therefore be well equipped for detecting high velocity motion. As far as I know, there have been only two studies of the upper limits of motion detection in infants (apart, of course, from the experiments to be described here). Both found that d_{max} (and thus presumably v_{max}) for discriminating coherent from incoherent motion in rdps decreased with age (Spitz & Kleffner, 1991; Kramer & Bertenthal, 1989). As for the v_{min} experiments discussed above, this task can be accounted for in terms of mechanism spatiotemporal tuning without invoking directional-selectivity (this point, and the results of these experiments, will be discussed in more detailed later on).

Directional motion mechanisms

As has been seen, the behavioural studies done to date offer rather limited and equivocal insight into the development of directional motion mechanisms in infants, despite the importance of these mechanisms for adult motion detection. The most direct evidence for cortical directional selectivity in infants comes from a visual evoked potential (VEP) study (Wattam-Bell, 1991) which formed the launchpad for the experiments to be described here. VEPs were recorded in response to periodic reversals in direction of a moving random-dot pattern. The direction reversals were embedded in a more frequent sequence of "incoherent jumps" produced by replacing the pattern with a new and uncorrelated rdp; these were introduced to mask the spatiotemporal transients associated with direction reversals which might otherwise have caused a response in non-directional mechanisms. In adults, two response components can be identified in this VEP; one at the frequency of the incoherent jumps, and another at the lower frequency of the direction reversals. The latter is specific to the changes in motion direction, and must therefore be derived from directionally-selective cortical mechanisms. A group of infants was tested longitudinally at two velocities, 5 and 20 deg/sec. While the jump component was present at an early age, the direction-specific

responses first appeared at 10 weeks on average at 5 deg/sec, and significantly later (12-13 weeks) at 20 deg/sec. These results suggest (a) cortical directional selectivity may not be present at birth, but emerges during the first weeks of life, and (b) it develops first at low velocities, spreading to higher velocities with age.

The development of smooth eye movements shows a pattern which is at least qualitatively similar to that revealed by the VEP results. Smooth pursuit is not found before 6-8 weeks (Aslin, 1981; contrary evidence of pursuit in newborns (Kremenitzer et al, 1979) is probably contaminated by OKN responses: see Aslin, 1987). At first, pursuit is only accurate at low velocities; accuracy at higher velocities improves with age (Aslin, 1981; Shea & Aslin, 1990). A similar picture is found for OKN. At birth, monocular OKN is highly asymmetrical, with little or no response in the nasal to temporal direction. Symmetrical mOKN appears at around 2 months (Atkinson & Braddick, 1981; Naegele & Held, 1982), and shows the same low-to-high velocity developmental trend (Mohn, 1989). Both pursuit (Lisberger et al, 1987) and nasal to temporal OKN (van Sluyters et al, 1991) appear to depend on cortical pathways, and it is not unlikely that their development reflects the maturation of directional mechanisms in these pathways. The temporal to nasal component of OKN, which is present at birth, is at least partly controlled by a direct subcortical projection from retina to NOT (van Sluyters et al, 1991); this pathway may represent the sole remains of the evolutionary and developmentally primitive motion system proposed by Horridge (1984).

Norcia et al (1991) have devised a novel VEP technique that can produce response asymmetries which suggest directional asymmetries in cortical motion processing. Like OKN asymmetry, the asymmetric component of the VEP is present with monocular viewing in young infants and patients with impaired binocular vision, is of opposite phase in each eye, indicating a nasal-temporal asymmetry, and decreases in the course of normal development, but more slowly at higher velocities. In other words there is good accord between the VEP and OKN asymmetries, which suggests that at least part of the latter reflects asymmetries in cortical as well as subcortical motion processing.

Motion cues in perception

Local motion detection is only the first stage in the use of motion information for

perception. As was discussed above, a more global view is necessary to resolve the ambiguities inherent in a purely local analysis. However global analysis of motion goes further than this; by combining local motion signals in a variety of ways the visual system can extract information about the layout and contents of the visual scene. Perhaps the most basic of these processes is image segmentation; motion information can by itself support the perceptual grouping of regions sharing a common motion, and the detection of boundaries between regions of different motion. There is evidence for these processes in quite young infants. For example, 3-month-olds can use motion-defined contours to extract information about the 2-dimensional shape of objects (Kaufmann-Hayoz et al, 1986). Likewise, Kellman and Spelke (1983) have shown that 4-month-olds can group the spatially separated parts of a partially occluded object which share a common motion; however in a similar experiment, Slater (1992) found no evidence of this grouping process in newborns. In all these studies the objects' motion was uniform (ie all parts moved with the same velocity) against a stationary background. Non-uniformities in an object's (projected 2-dimensional) motion can also provide shape information ('structure-from-motion'). Here the picture with infants is not so clear. At 3 months infants can distinguish between rigid and non-rigid motion of an object (Gibson et al, 1979). Arterberry & Yonas (1988) have shown that 4-month-olds are capable of quite subtle form discrimination in 3-dimensional structure from motion displays using random dots. However, Spitz et al (1992) found that infants were apparently unable to extract 2-dimensional structure from non-uniform motion (rotation and expansion in random dot patterns) until around 7 months.

While it is not always certain exactly which cues are used by infants in these kinds of motion-based perceptual tasks (and whether they are the same as the cues used by adults), the overall impression from such experiments is that by 3-4 months low-level motion processing is quite mature and able to support relatively sophisticated perceptual functions. Unfortunately there have few such studies on younger infants, and little is known about the early development of these abilities. A notable exception is the work of Slater (1992) cited above indicating that newborns are unable to group spatially separated regions which share a common motion.. Slater et al (1985) have also examined the complementary question - the extent to which motion can interfere with newborns' shape perception. They found that although the infants could extract shape

information from rotating objects, they were unable to generalise this information between rotating and static displays, though they could generalise between translating and static displays. They also found that newborns did not distinguish between clockwise and counter-clockwise rotations of a single object, which suggests they are insensitive to direction of motion.

Overview

At this point it is possible to sketch a tentative picture of the development of low-level motion processing. At birth, motion detectors operate only over a very restricted velocity range. This range expands during development as a result of increasing sensitivity to both low and high velocities. Moreover, the only directional motion mechanisms in the newborn visual system may be those in the subcortical nuclei involved in the control of OKN, and these are unlikely to contribute directly to perception. The VEP results demonstrate that cortical directional selectivity is present by 10 weeks, while the pursuit data suggests that it emerges slightly before this, say between 1 and 2 months of age, and a variety of evidence suggests it develops first at low velocities, spreading to higher velocities later. This places the onset of directional selectivity midway between that of two other characteristic cortical response properties, orientation-selectivity, which is present at birth (Atkinson et al, 1988; Slater et al, 1988), and binocularity, which develops at around 3-4 months (Braddick & Atkinson, 1983). A speculative account of this timetable suggests that it reflects an early maturation of the parvocellular system, followed by more delayed development in the magnocellular system (Braddick, 1993a; Atkinson, 1993). The response properties characteristic of (though probably not exclusive to) the magnocellular system - directional selectivity, particularly at higher velocities; sensitivity to binocular disparity; sensitivity to high temporal frequencies and bandpass temporal tuning - all appear to take-off at around 3 months. If, as suggested above, directionality at low velocities emerges somewhat earlier than this, then it may represent the development of the distinct low-velocity (parvocellular?) motion system discussed above.

This developmental picture is evidently vague, speculative, and to a large extent based on indirect evidence. This thesis aims to provide direct behavioural data on the development of motion mechanisms, and in particular directional mechanisms, in order

to gain a more concrete understanding of the development of low-level motion processing in infants. The main questions are:

(a) How do the upper and lower velocity limits for directional responses change during development?

(b) What do these changes tell us about the development of the spatial and temporal parameters (ie ΔS and ΔT - Fig 1.2) in the population of motion mechanisms?

(c) When does cortical directional-selectivity first emerge? Is it already present at birth, and if not, does it develop before other visual functions which are considered to be characteristic of the magnocellular system?

(d) How do the more global aspects of motion processing, such as the spatiotemporal integration discussed above, develop during infancy? This is clearly a large topic, and the experiments on it described here represent little more than a preliminary skirmish with it.

This study, then, is directed towards understanding the development of the functional properties of, and interactions between, low-level cortical motion mechanisms. Experience suggests that the most interesting changes in low-level visual mechanisms occurs in the first six months of life, and this is the period focussed on here. The experiments are all behavioural, and, since the aim is to chart infants' progress towards adult performance, their design draws extensively on relevant adult studies. These are of course rarely designed with infants in mind, and are usually impossible to replicate exactly with infants. Hence an important part of the present work consists of adult experiments done under identical conditions to the infant experiments, which are intended to form a bridge between the infant results and the adult literature. Random-dot patterns (rdps) are used as stimuli throughout. Rdps have been widely used in adult experiments; one reason for their popularity is that positional cues to motion (ie the kind of cue which is used to infer the motion of the hour hand of a clock) are very effectively disguised in them (see Fig 1.1). For the most part, the experiments explore infants' ability to detect a region of random dots undergoing one kind of motion (the target), embedded in a background of random dots undergoing a different kind of motion. For adults, such displays result in segregation of target and background, usually with sharp boundaries between them. Most of the experiments simply use

detection of the target as an index of infants' ability to discriminate between the different kinds of motion in the target and background, and do not directly address the question of whether infants also see them as segregated, and more generally of what cues infants use to detect the target. However these are clearly important questions, and are considered in detail below.

2 Methods

Stimuli

The stimuli used in these experiments were random-dot patterns (see Fig 1.1). They were generated by a computer and displayed on a video monitor. The computer updated the patterns between every video frame (ie every 20 msec). In general, this update could take one of three forms:

1. *Static:* The pattern was not changed.
2. *Coherent displacement/coherent motion:* The pattern was coherently displaced by a given amount in a given direction. Note that the borders of the pattern were not displaced; for example with a leftward shift, elements moving beyond the left border disappeared, while the gap created inside the right hand border was filled by new random dots. In general this update rule leads to the appearance of a coherently moving pattern viewed through a fixed window.
3. *Incoherent jump/incoherent motion:* The pattern was replaced by a new and uncorrelated random-dot pattern. This produced spatiotemporal noise which appeared as incoherent local motions in all directions, but with no overall direction or speed.

Rule 2, in which a pattern is replaced by a coherently displaced version of itself, produces apparent motion. Many adult studies have measured performance for single isolated displacements of this sort. However this inevitably results in trials of short duration which are hopeless for infant work, and the experiments described here all used extended sequences of coherent displacements. Unlike single displacements, sequences have a well-defined velocity (=displacement size/displacement interval). The minimum displacement interval was 20 msec (the monitor's frame period); longer intervals could be produced by inserting static updates (rule 1) between displacements. Evidently the coherent motion can be characterised either by its velocity or displacement size, and both are used here; when displacement is given it is always the size of the individual displacements which make up a sequence. Displacement size and interval were never changed in the course of a sequence.

The computer could divide the screen into a set of non-overlapping rectangles,

each containing a random-dot pattern. All rectangles were updated at the same time, though not necessarily with the same rule. The borders between rectangles coincided with the edges of the rdp elements; hence the borders between adjacent rectangles with the same spatiotemporal behaviour (ie the same update rule) were not visible. However if there is some form of motion contrast between rectangles, such as coherent vs incoherent motion, or different directions and/or speeds of coherent motion, then adults see them as clearly segregated, with sharp borders between them.

Pilot experiments using preferential looking (see Chapter 3) revealed that infants are also sensitive to motion contrast; they consistently prefer to attend to regions containing motion contrast over spatiotemporally uniform regions. This observation provides a foundation for much of the work described here.

Several important aspects of the stimuli, such as the way that the rdps were generated and the layout of rectangles on the screen, were varied according to the needs of particular experiments and will be detailed in the description of the experiments. However a number of features were common to all experiments. An Acorn Archimedes computer generated the stimuli and controlled the experiments. The stimuli were displayed on a large screen video monitor (Bluebest 24in monochrome or Mitsubishi 26in colour). Subjects viewed the screen from a distance of 40 cm and the area in which rdps could be displayed was 48 deg wide by 39 deg high. This whole area was not always filled with rdps; some rectangular regions could instead be uniformly illuminated. The random-dot patterns were generated from black and white square elements (sides subtending 0.32, 0.48 or 0.64 deg - note that any given display contained elements of one size only). Unless otherwise stated, luminance of the black elements was 0.9 cd/m^2, and of the white elements 14.3 cd/m^2, giving a contrast of 88%.

In coherently moving regions of the stimulus, the direction of motion periodically reversed. For example, horizontal motion consisted of a sequence of n coherent displacements to the left, followed by n displacements to the right, then a further n to the left, and so on until the end of the trial. The usual value of n was 12, ie 240 msec between direction reversals with a displacement interval of 20 msec. There were two main reasons for using this oscillating motion. First, it made the stimulus comparable with that used in the VEP study (Wattam-Bell, 1991); one aim of the present

experiments was to corroborate the findings of that study using behavioural methods. Second, and more important, oscillating motion largely eliminates ocular tracking of the stimulus. Tracking a moving pattern reduces its retinal velocity and hence the amount it is blurred, while increasing the retinal velocity and blurring of patterns moving in other directions. This can introduce an effective (luminance) contrast difference, ie a non-motion cue for discrimination.

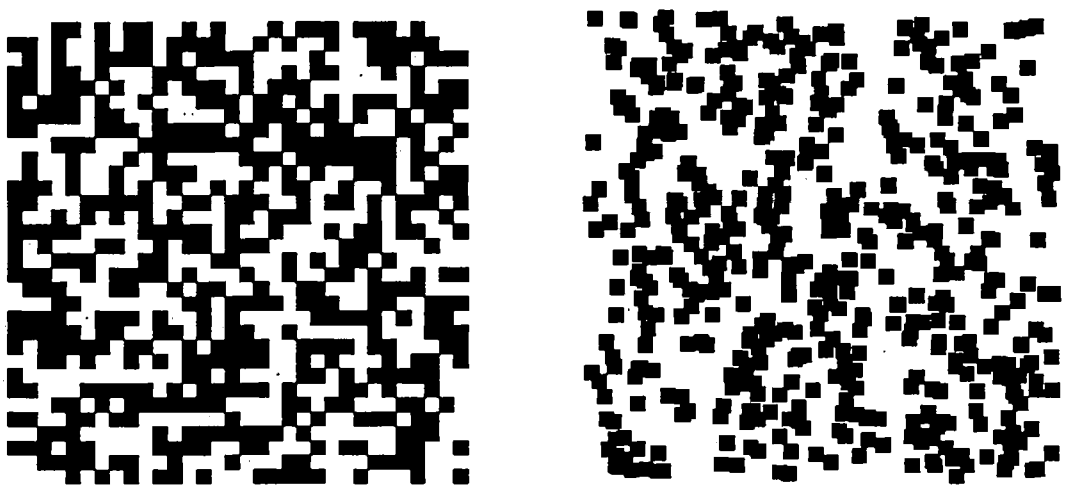

Fig 2.1 Type 1 and Type 2 random-dot patterns. Note that the type 2 pattern shown here is made up of black elements on a white background, whereas on the video display these patterns consist of white elements on a black background.

The experiments used one of two types of random-dot pattern (Fig 2.1). The difference between them is best understood in terms of recipes for making them.

Type 1: Divide the rectangle in which the pattern is to be drawn into a regular grid of squares, each the size of an rdp element. For each square, toss a coin to decide whether the rdp element drawn there is black or white. This results in a rdp whose elements are aligned horizontally and vertically. On average there are equal numbers of black and white elements. Coherent motion involves shifting the underlying grid, thus displacing the whole pattern. This shift can be smaller than the size of an element; elements extending beyond the boundary of the rectangle are chopped off at the boundary. Incoherent jumps are produced by replacing all elements in another round of coin-tossing.

Type 2: First, colour the whole rectangle black. Take a handful of white rdp elements

and scatter them over the rectangle, ensuring that no part of any element falls outside the boundary. In this type of rdp, the elements are not aligned, and in general there are unequal amounts of black and white. A coherent displacement is achieved by moving each white element by the same amount in the same direction; for an incoherent jump, all the elements are picked up and scattered again over the rectangle.

In type 2 patterns (but not in type 1), element positions are independent of each other. This means that different elements can behave in different ways; for example, a fraction of the elements can be coherently displaced, while the rest are randomly repositioned (incoherent jump). This option of having a variety of dynamic patterns simultaneously in any one region of the stimulus is the fundamental reason for using type 2 patterns. It is not possible with type 1 rdps.

As in all computer graphics systems, the patterns are drawn on an underlying array of screen pixels. Each rdp element spans a number of pixels horizontally and vertically; this number depends on both element size and screen pixel resolution. The latter is determined by the Archimedes computer, which offers a variety of graphics modes with different resolutions; the two used here were 640 (horizontal) x 256 (vertical) and 640 x 512 (these are the numbers of pixels in the whole 48 x 39 deg stimulus area).

In the simplest case, each pixel is either black or white. Evidently this constrains the edges of the rdp elements to lie on the border between pixels, so that the smallest coherent displacement (and thus lowest velocity) is determined by distance between adjacent pixels, while larger displacements must be an integer multiple of this value. It is possible to overcome this constraint by using sub-pixel positioning (described in Appendix 1), which allows much smaller minimum displacements and velocities, and this approach was used in some of the experiments.

Procedures

The behavioural methods most widely used in infant vision research are forced-choice preferential looking and habituation. Both were used in the present study.

Forced-choice preferential looking (FPL)

Forced-choice preferential looking (Teller, 1979) is the standard way of doing

psychophysics in infants. It is a variant of the spatial two-alternative forced choice technique which is commonly used in adult psychophysics. The infant is seated in front of the stimulus display and is observed by an adult who is concealed behind the display. Between trials the display contains, in addition to the random dots, a centrally located column of flashing or drifting rectangles which is designed to attract the infant's attention to the midline. When the infant is fixating the midline, the observer presses a switch which instructs the computer to initiate a trial. The central fixation stimulus is then removed, and the stimulus to be detected appears either on the left or the right of the midline; the side is chosen randomly by the computer. The observer, who can't see the stimulus, makes a forced choice about which side it lies based on the looking behavior of the infant and indicates this choice by pressing one of two switches (should the infant become fretty, or look away from the display, the observer can press a third switch which cancels the trial). In these experiments the stimulus to be detected consisted of a rectangle of coherent motion (the target) surrounded by rectangles of some contrasting dynamic behaviour (the background - usually either incoherent motion, or coherent motion in the opposite direction to the target's). The non-stimulus side of the display contained a uniform region with same dynamic behaviour as the background.

If the infant's looking behaviour is random, ie not determined by the stimulus, he/she will on average look towards the side with the target in half of the trials - a performance of 50% correct. A performance that is significantly above 50% correct (consistent looking towards the target) is direct evidence that the infant can discriminate between target and background. Beyond simply demonstrating discrimination, FPL can be used to determine thresholds for various parameters of motion, such as velocity, ie the value at which performance declines from some high level (say 90% or above) towards chance. In this work, thresholds were taken as the parameter value giving approximately 70% correct. This was estimated using one of two staircase procedures which were run automatically by the computer controlling the experiment. The procedure of choice was the 2-up/1-down staircase of Wetherill and Levitt (1965); however under certain circumstances this can produce spurious results, and in some experiments a more robust but less efficient staircase was used. Both procedures are described in detail in Appendix 2, which also includes an account of the

problems that can arise when using staircases with infants.

Habituation

The success of FPL depends not only on the infant's ability to discriminate target from background, but also on an intrinsic preference for the target (or the target/background contrast). No preference does not necessarily imply no discrimination. In a threshold experiment, a decline in performance (of a single infant) from near 100% to chance as, say, velocity is increased is a strong indication of reduced discrimination at high velocities; however, chance performance in young infants for some stimulus configuration which elicits good performance in older infants is at best weak evidence for a failure of discrimination by younger infants. Hence the need for habituation, which is the method of choice for testing infant discrimination when there is no intrinsic preference. Essentially it involves attempting to induce a preference for one of a pair of stimuli by habituating the infant with repeated presentations of the other member of the pair. After habituation, looking times to the old and new stimuli are compared; a preference, and thus discrimination, is indicated by the infant looking longer at the new stimulus.

A habituation experiment has two phases. The first, infant control habituation (Horowitz, 1975), proceeds as follows. At the start of a trial the infant is turned to face the screen, which is blank apart from a central fixation stimulus. When the observer judges that the infant is fixating the central stimulus, he/she presses a button to start the trial proper. The computer removes the fixation mark and displays the habituation stimulus. Looks away from, and back to, this stimulus are recorded by further button presses, and the trial continues until the first look away that lasts more than 2 sec. The infant is turned away from the screen for a short period (about 5 sec) and then turned back for the next trial. For each trial the computer records the total time that the infant spent actually looking at the stimulus. It also calculates the mean looking time of each possible set of three consecutive trials, and the habituation phase continues until this mean time has fallen to 50% or less of its previous peak value, with the proviso that these last three trials do not overlap with the three contributing to the peak. Once this criterion has been reached the test phase is entered. Test trial procedure is similar to the habituation trials, but now the display contains the habituation stimulus on one side,

and the novel stimulus on the other. The observer's button presses record the onset of looks towards either of the two patterns, or away from both. The test trial continues until total time spent looking at the stimuli reaches 20 sec. There are two test trials; in the first the location of the habituation and novel stimuli are chosen at random while in the second their positions are reversed.

Habituation is a powerful technique which has been used with considerable success to investigate visual discriminations in newborns and older infants (eg Atkinson et al, 1988; Braddick et al, 1986; Slater et al, 1988). Its singular, and very important advantage over FPL lies in its ability to demonstrate discrimination between two patterns in the absence of a preference for either. However it has a number of disadvantages. A single habituation run takes about as long as one or two complete FPL threshold estimates (40 - 100 trials), so that in general only one or two habituation runs are possible in any one visit. Moreover an individual infant's results have no statistical validity; habituation can only be used to assess performance of a group of infants (usually defined by a particular age range).

For both habituation and FPL experiments, the display was surrounded by grey card, and beyond this by grey curtains. Room lighting was adjusted to make the luminance of the surround and the screen roughly the same. As well as providing a neutral environment to encourage the infant to attend to the display, the surround hid the observer, who viewed the infant through a small peephole immediately above the display monitor.

The infant was seated on lap of a holder who was a member of the VDU staff. The holder was responsible for keeping the infant in as calm and alert state as possible during testing, for keeping the infant at the correct viewing distance with his/her head centred on the display, and when necessary for directing the infants' attention to the fixation stimulus. In addition it was important for the holder, who had a clear view of the stimulus, to avoid any action which might bias the infant's looking behaviour during a trial. The success of behavioural infant testing depends to a considerable degree on the skill and experience of the holder.

In experiments involving more than one threshold estimate, or more than one habituation run, infants were given a break of several minutes between tests. If it was

not possible to complete testing in one visit, a second visit was arranged no more than 7 days later. When testing was restarted after a break or on a second visit, unfinished threshold estimates and habituation runs were always started again at the beginning.

Adult experiments

The adult experiments employed a spatial two alternative forced choice design using the same equipment, stimuli, and viewing distance (40 cm) as the infants. The subjects themselves pressed the switches to indicate their left-right choice. A stationary fixation marker was displayed throughout, and subjects were instructed to keep looking at it. Trials were not initiated by a switch, but instead started automatically 1 sec after the subject had responded to the previous trial. Fixed stimulus durations (usually <1 sec) were used, after which the display reverted to its between-trial state while the computer waited for a response. The staircase procedures used to estimate infant thresholds (see Appendix 2) were also used with the adult subjects.

Subjects

The infant subjects were children of volunteers living in the Cambridge area who were recruited by leaflet from the maternity hospital. Only infants born within 14 days of term, and with no known ocular or other abnormality, were included in the study. The results reported here were obtained from a total of 276 infants aged between 3 and 16 weeks (though no single experiment spanned this whole range). These were just the successfully tested subjects; as in all infant research, a considerable number of infants were seen who failed to complete testing because of fussing or sleepiness. Success rates in individual experiments are not reported; these varied from around 40% to 70%, and were generally lower in the experiments on the youngest infants.

All ages reported are post-term ages and are given in weeks; thus for example a 10-11-week-old group consists of infants who were tested somewhere between 10 weeks, 0 days and 11 weeks, 6 days after their expected date of birth.

The author was the main adult subject. However a number of other adults, all members of staff at the VDU, were also tested. All had normal or corrected to normal vision.

3 Discrimination of coherent from incoherent motion

The first experiments on motion processing in infants examined their ability to discriminate between coherent and incoherent motion. These were forced-choice preferential looking (FPL) experiments. The stimulus used type 1 rdps constructed from 0.32 deg elements. The target was a vertical strip undergoing coherent vertical motion whose direction reversed every 240 msec, flanked by regions of incoherent motion. The intervals between coherent displacements, and between incoherent jumps, were both 20 msec; with the underlying pixel resolution of 640 x 256, the smallest coherent displacement was 0.16 deg, giving a minimum velocity (and smallest velocity increment) of 8 deg/sec. Between trials the display was filled with incoherently moving dots, with a vertical column of rectangles at the centre as a fixation marker. Fig 3.1 gives full details of the stimulus.

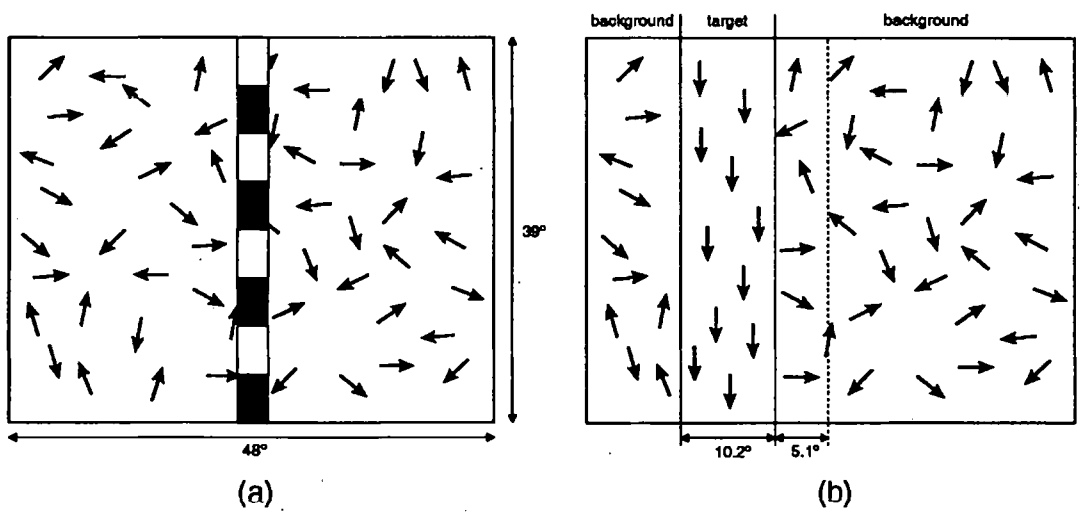

Fig 3.1 Schematic illustration of the stimulus. (a) shows the display between trials, with the central column of rectangles which was used to attract the infants' attention to the midline. Incoherent motion of the rdp is indicated by the randomly oriented arrows. (b) shows the display during a trial. The fixation target has been removed, and a target region of coherent vertical motion, indicated by the vertically aligned arrows, has appeared against a background in which the dots continue to move incoherently. The target is shown here on the left, and moving downwards; in practice the side on which it appeared was chosen randomly from trial to trial, and its motion alternated periodically between upwards and downwards.

Pilot experiments

At this stage, it was by no means certain that this (or any motion contrast) stimulus would be effective in an FPL experiment on infants. Preferential looking was developed for the assessment of acuity and contrast sensitivity; ie detection experiments, in which a grating on one side is paired with a uniform field on the other, and it is not surprising that infants look towards the pattern if they can see it. However the present experiments involve discrimination, and there is plenty to attract an infant's attention on both sides of the display.

The first step, then, was a pilot experiment on a group of seven 2-3-month-olds. They were tested with target velocities of 8 and 16 deg/sec, both of which gave good target/background segregation for adult observers. This experiment demonstrated that it was possible to obtain a consistent preference for the target side (70-100% correct out of 10 or more trials). It also revealed some of the factors which were important for achieving good performance. First, some of the infants produced apparently random looking behaviour for the first few trials, before settling down to consistent looks towards the target. While part of this warm-up period depended on the observer getting acquainted with the infant's style of response, in many cases it also seemed to involve the infant 'tuning in' to the interesting parts of the display. As a result of this finding, all subsequent FPL experiments were started with a set of at least 5 warm-up trials. The second important factor concerned the pattern of looking behaviour shown by infants. In a preferential looking experiment the observer is in principle free to use any cue from the infant's behaviour. More obvious examples include direction of first fixation, relative frequency of fixations to left and right, and relative duration of looks to left and right. Surprisingly, it rapidly became obvious that direction of first fixation was far and away the most reliable cue, and for the majority of trials in all the FPL experiments described here the observer's response was based on this cue. This meant that trials were short, which allowed plenty to be packed into a session. Although there was no fixed limit on the duration of a trial, most lasted less than 2 sec and, with the exception of the experiments on one-month-olds described later, none lasted longer than 10 sec.

The finding that infants can discriminate target from background naturally leads to the question of what they actually see in the stimulus. Are they responding to a

clearly segregated target with a well-defined boundary between it and the background, or simply to the less uniform dynamic behaviour on the target side? The prompt and reliable response to the target indicates that it is highly salient and suggests that they do indeed see a clear segregation. Some of the experiments to be described in later chapters provide a degree of insight into this question, and it discussed more fully there. Meanwhile it is important to note that while it seems quite likely that infants are responding to segregation of the target, logic alone does not force this conclusion.

d_{max} for discrimination between coherent and incoherent motion

As the velocity (displacement size) of the coherently moving target is increased, the motion appears progressively less coherent. At sufficiently high velocities the sense of coherent motion breaks down completely and it becomes indistinguishable from the incoherent motion of the background. Inevitably this must occur for displacements greater than or equal to the size of the patch, since such displacements result in a sequence of completely uncorrelated rdps. However in practice the breakdown occurs at much smaller displacements; it represents a psychophysical rather than a physical limit - d_{max} (Braddick, 1974).

d_{max} was measured in infants by varying displacement in steps of 0.16 deg according to the bracketing staircase procedure, which seeks to place trials so that they bracket the displacement giving a performance of 70% correct. This staircase is described in Appendix 2. It terminates when it has found a pair of displacement levels, separated by 0.16 deg, for which performance is ≥70% at the lower level, and <70% at the higher. The displacement giving 70% correct (d_{max}) is then found by linear interpolation. The staircase will also terminate if it fails to find a level at which performance is 70% or better, but this never happened in the present experiment.

The same staircase was used to determine d_{max} in adults. Trial duration was fixed at 0.48 sec (one complete cycle of the target's up/down oscillation), and the subject was instructed to fixate the central marker throughout the trial. This procedure was chosen in attempt to equate conditions between adults and infants. Although in principle unlimited, in practice trial duration for infants was typically 1-2 sec. Since this included both the infant's saccadic and the observer's manual reaction times, the infant's response must have been based on a considerably shorter exposure to the stimulus. The choice of

0.48 sec for adults as a match for the unknown effective trial duration for infants was based on preliminary tests which indicated that adults' d_{max} was independent of trial duration in the range 0.24-1.68 sec. With infants, trials started with the subject fixating the centre of the display, and as discussed above the usual response criterion was the direction of the first fixation away from the centre. Evidently then infants for the most part detected the target when it was in the peripheral visual field, approximately at its nominal eccentricity of 5-15 deg (see Fig 2.1). The instruction to maintain central fixation ensured that the same was true for adults.

Results were obtained from 23 infants and 3 adults. The infants were divided into three age groups: 9-10 weeks (n=8), 11-12 weeks (n=7) and 13-16 weeks (n=8). The group results are shown in Fig 3.2, where it can be seen that infants' d_{max} increased with age; analysis of variance revealed that the effect of age was significant ($F(2,20) = 5.78$, $P < 0.01$). The rise in d_{max} must continue well beyond 13-16 weeks, since the mean d_{max} for this group was less than one-third of the value obtained from adults.

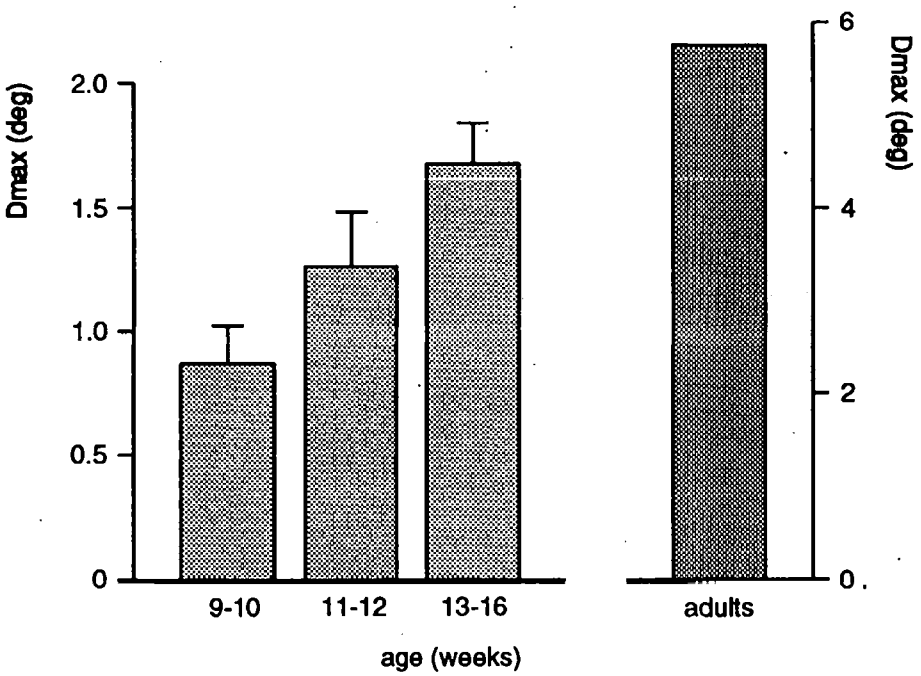

Fig 3.2 Mean d_{max} (+1 standard error) for discrimination of coherent from incoherent motion from the three groups of infants, and for the adult subjects. Note the different scale used for the adult data. Individual results are given in Table 1 of Appendix 4.

Of the experiments described in this thesis, the present one most closely approximates the conditions under which Kramer & Bertenthal (1989) and Spitz & Kleffner (1991) measured d_{max} in infants. However the present results appear to be

quite at odds with their findings. Both studies used preferential looking to measure d_{max} in random-dot patterns. In Kramer & Bertenthal's experiment infants chose between a display containing alternating stripes of coherent and incoherent motion and another containing only incoherent motion; a stimulus which is broadly similar to the one used here. They found that d_{max} decreased with age, from 0.55 deg at 12 weeks to 0.37 deg at 20 weeks. Their 12-week d_{max} is less than half the value found here for infants of similar age (Fig 3.2). Moreover it is substantially less than the likely values of adults' d_{max} with their stimuli[6]. In other words it is likely that the modest fall in d_{max} between 12 and 20 weeks reported by Kramer & Bertenthal is superimposed on a much larger increase between infants and adults.

Spitz & Kleffner (1991) measured d_{max} for motion coherence using a three alternative forced-choice between three patches of random dots each of which moved coherently, but with different displacement sizes. Initially they found that 4- and 7-month-old infants preferred displacement sizes of 2 deg and below to larger displacements, whereas for adults all displacements above 1 deg appeared equally incoherent and indiscriminable. In a later experiment, they found that a modest decrease in rdp element size (from 0.5 to 0.33 deg) reduced 7-month-olds' d_{max} to 1 deg, the same as for adults. They attributed the superior performance of infants in the first experiment to their detection of a "local motion helix" which adults saw in the patterns with the larger elements when these were low-pass spatially filtered.

There is no obvious explanation for the discrepancy between the present results and those of Kramer & Bertenthal (1989) and Spitz & Kleffner (1991). However, as will be seen below, there is considerable doubt about how much experiments on the discrimination of coherent from incoherent motion actually reveal about motion processing, and this issue will not be pursued further.

At first sight, the ability to discriminate between coherent and incoherent motion might seem to be the hallmark of a true motion analysing system (whatever precisely

---

[6]Kramer & Bertenthal do not report this. However with their stimuli adult d_{max} should be well over 1 deg. One of the most important determinants of d_{max} is stimulus eccentricity, and in their displays regions of coherent motion extended at least 18 deg into the periphery. For comparison, Baker & Braddick (1985a) found values of around 1.5 deg at 10 deg eccentricity, while in the present experiment, which used more comparable stimuli (but with the target only extending out to 15 deg), adult d_{max} was around 6 deg.

that means), and the results shown in Fig 3.2 appear to confirm the suggestion made in the introduction that the upper displacement/velocity limit of infant motion detectors increases with age. Before accepting this, though, it is worth asking exactly what kind of visual mechanisms might be involved in discriminating between coherent and incoherent motion. The first point to note is that it does not logically depend on knowing the direction of the coherent motion. Thus in principle directionally selective mechanisms are not required; evidence that this is also true in practice is presented below. In fact it is quite straightforward to demonstrate that the minimum requirement is for mechanisms which act as low-pass spatial and temporal filters, or indeed more generally mechanisms which have finite upper spatial and temporal frequency limits (which includes band-pass as well as low-pass responses). A mechanism's upper spatial frequency limit is inversely related to the size of its receptive field. For displacement sizes that are appreciably smaller than the receptive field, the response to successive coherent displacements will be highly correlated. This temporal correlation means that most of the energy in the response is at low temporal frequencies, and will be relatively unaffected by low-pass temporal filtering. With incoherent motion the temporal correlation is absent; in this case the response energy spreads out to high temporal frequencies, and is more severely attenuated by low-pass temporal filtering. Thus the combination of low-pass spatial and temporal responses results in a mechanism which responds more vigorously to coherent than to incoherent motion. In addition, this difference in responsiveness diminishes as the speed (displacement size) of the coherent motion increases (see Appendix 3, which gives a more complete and rigorous account of this argument). This means that there will be some displacement size beyond which the responses to coherent and incoherent motion will be indistinguishable. In this scheme, d_{max} is an increment threshold - a measure of the smallest detectable increase in the response of these mechanisms above that produced by incoherent motion. The rise in d_{max} with age could be a result of an increasing sensitivity to small increments, analogous to the improvements in contrast increment thresholds during development (Stephens & Banks, 1987). However there is another, related, possibility. Discrimination at high speeds could also be improved by increasing the difference in response to coherent and incoherent motion. This can be achieved by more severe low-pass spatial filtering, ie by integrating over larger areas of the stimulus (Appendix 3).

The rise in d_{max} may result from the development of mechanisms with larger receptive fields. At first sight this notion flies in the face of a large body of research demonstrating a progression from coarse to fine spatial scales during development. However there is (as far as I know) no direct evidence against it.

It seems then that the discrimination of coherent from incoherent motion, the existence of a displacement limit (d_{max}) for this discrimination, and the increase in d_{max} with age, can all be accounted for in terms of mechanisms with limited sensitivity to high spatial and temporal frequencies. Now the constraints of physical realizability (not to mention the wealth of psychophysical and physiological data) demand that all visual mechanisms are limited in this way. The stimuli used here [and, by precisely the same argument, those used by Kramer & Bertenthal (1989) and Spitz & Kleffner (1991)] may not be providing information specifically about the motion pathways of the visual system. One way of looking at this is that at least in principle some useful motion information can be extracted by mechanisms outside this pathway. However the adult visual system undoubtedly has mechanisms and pathways specialised for motion analysis, and these are the natural focus of interest when investigating the development of visual motion processing. A different approach is needed.

4 Discrimination of motion direction

Sensitivity to direction plays a key role in motion perception, and is the most commonly used psychophysical and physiological criterion for motion sensitivity. A major advantage of focussing on direction is that it is about the only parameter of motion that can be changed without altering the spatiotemporal frequency spectrum of the stimulus[7]. As was seen in the last chapter, experiments on discrimination of motion parameters such as coherence or speed, which result in different spatiotemporal spectra, do not necessarily tell us anything specific about the development of motion processing. The present chapter describes experiments on infants' sensitivity to direction of motion. An unchanging spatiotemporal spectrum is strictly only found between opposite directions of motion, and it is this discrimination which is examined here. The stimuli were identical to those used in the previous experiment, except in one important respect; the background did not undergo incoherent motion, but instead moved coherently at the same speed as, but always in the opposite direction to, the target. This configuration also results (for adults) in clear segregation of target and background. Now, however, the only cue supporting this segregation, and more generally detection of the target, is the difference in direction of motion between target and background.

d_{max} for discrimination of opposite directions of motion

d_{max} for direction discrimination was measured using the bracketing staircase in 58 infants and two adults. The infants were aged between 8 and 15 weeks, and were divided into four age groups, each spanning 2 weeks. The number in each group is shown in Fig 4.1(a). An appreciable number of infants did not achieve a performance of 70% or more correct at any displacement tested. For these infants, trials cycled through the three smallest displacements (0.16, 0.32 & 0.48 deg) until 15 trials had been obtained at each level. Provided the infant was calm and alert throughout the

[7]The spectrum gives only the amplitudes of the frequency components in the stimulus. In order to discriminate between opposite directions of motion, information about the relative phases of these components is needed.

session, and performance remained below 70% at these levels, then the data were taken as evidence that d_{max} for that subject was below 0.16 deg. All but one of these infants were in the youngest (8-9 week) group - see Fig 4.1 (a).

The group results are shown in Fig 4.1(b). As was the case for the coherent/ incoherent discrimination results of the previous chapter, d_{max} for direction discrimination increased with age, and this effect was highly significant (Kruskall-Wallis anova, $P < 0.001$). Again, comparison of the oldest group with adults indicates that the rise in d_{max} continues well beyond 14-15 weeks.

In all age groups, the majority of infants showed clear evidence that they could discriminate between opposite directions of motion, which implies that by 8-9 weeks there are functional directionally-selective mechanisms in the infant visual cortex. What about the 42% of 8-9-week-olds who failed to show evidence of direction discrimination? Their results have been included in Fig 4.1 on the assumption that d_{max} was below the smallest available displacement of 0.16 deg - ie that d_{max} would have been measurable had it been possible to test them with smaller values. This assumption is compatible with the increase in d_{max} with age, and is supported by the finding that while individually none of these infants performed above chance, as a group their performance was significantly better than 50% at 0.16 deg (Wilcoxon test, $P < 0.05$), but not at 0.32 or 0.48 deg (see Appendix 4, Table 2b). Nevertheless it remains possible that some 8-9-week-olds are unable to discriminate direction at any displacement; it may be that cortical directional selectivity first emerges at around this age, and is not present in younger infants. This issue will be pursued further in chapter 5. Meanwhile it is important to note that the significant effect of age on d_{max} does not depend on including the low-performing infants in the younger groups; as inspection of Fig 4.1(b) suggests, the effect of age is equally significant when the 8-9 week group, and the single infant whose performance was below 70% in the 10-11-week group, are dropped from the analysis.

What does the increase in d_{max} with age tell us about the development of directional motion mechanisms? As displacement increases, a progressively smaller fraction of the visible stimulus energy will signal the true speed and direction of motion. d_{max} may represent the point at which this fraction becomes too small to be detected; in terms of the archetypal motion detector of Fig 1.2, d_{max} may be determined

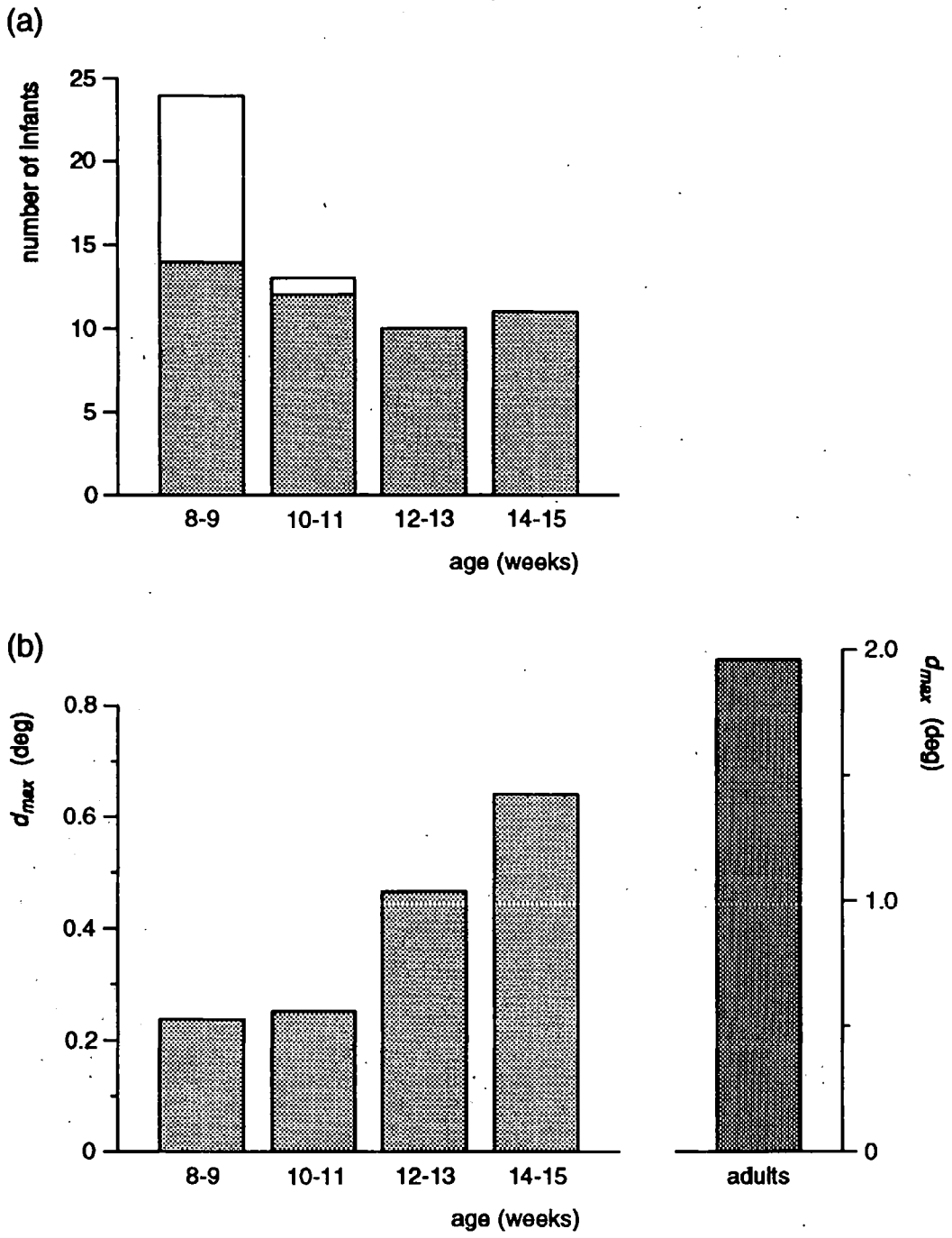

Fig 4.1 Development of d_{max} for direction discrimination. (a) The overall height of the columns show the number of infants in each age group, while the unfilled parts show the number in each group for whom d_{max} was less than 0.16 deg. (b) Median values of d_{max} from infants and adults. Note the change of scale between the infant and adult data. Individual results are given in Table 2a of Appendix 4.

by the sensitivity of the peripheral mechanisms (A and B) which act as inputs to the directionally-selective stage (C). In other words, infants' d_{max} may depend on their contrast sensitivity, and the age-related rise in d_{max} may reflect improving contrast

sensitivity rather than specific changes in the motion pathways of the visual system.

The effect of contrast on d_{max}

If contrast sensitivity determines d_{max}, then reducing stimulus contrast should reduce d_{max}. The next experiment examined this possibility. d_{max} was measured in eleven 10-11-week-olds and one adult subject for stimulus contrasts of 48% and 88% (the latter was the contrast used in the previous experiments). Mean luminance did not change with contrast. Each infant was tested with both; six saw the low contrast first, while the other five saw the high contrast first.

The infants showed a slightly higher d_{max} at the lower contrast (Fig 4.2), but the difference was not significant ($t = 0.53$, $P > 0.5$). The adult subject gave a similar result

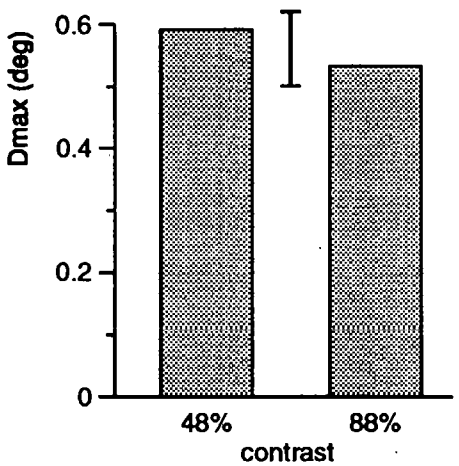

Fig 4.2 The effect of stimulus contrast on d_{max} for direction discrimination in a group of eleven 10-11-week-olds. The error bar shows the standard error of the mean of individual differences in d_{max} at the two contrasts. Individual results are given in Table 3 of Appendix 4.

(2.40 deg at 48%, and 2.32 deg at 88% contrast). Evidently contrast sensitivity does not determine d_{max} in either 10-11-week-olds or adults, and it is very unlikely that older infants would give a different result. One surprising aspect of the results is that the infants' mean d_{max} was about twice that obtained from the same age group under identical conditions in the previous experiment. It is possible that the infants in the present experiment were particularly mature; there is likely to be considerable individual variation in maturity around this age, and this group's d_{max} was comparable to that of infants in the previous experiment who were only two weeks older.

It seems that the development of d_{max} results from changes occurring at the level

at which directional responses are generated. What might these changes be? First, note that displacement and velocity covary in the stimuli used here. Although the results have been given as displacement limits, they could equally well have been expressed as velocity limits (v_{max}). A plausible account of the results is that younger infants lack directional mechanisms sensitive to high velocities, and that these emerge during the course of development. A mechanism's velocity sensitivity is a function of both its span, ΔS, and its delay, ΔT (see Fig 1.2), and changes to either of these could underlie the emergence of sensitivity to high velocities

The effect of displacement interval on d_{max}

Displacement size and velocity can be dissociated by changing the interval between successive displacements. For a given displacement, doubling the interval halves the velocity. The effect of such changes on d_{max} should indicate whether infants' performance is limited by displacement or velocity, and provide some insight into the relative importance of changes in the spatial and temporal properties of motion mechanisms in the development of sensitivity to high velocities. The next experiment compared d_{max} at displacement intervals of 20 and 40 msec. Two age groups were tested; 8-11 weeks (13 infants) and 12-15 weeks (12 infants). Each infant was tested under both conditions, and the order in which they were presented was counterbalanced (as far as possible) across subjects.

At 20 msec displacement interval (the interval used in the previous experiments), the 8-11 week infants performed rather worse than their counterparts in the first experiment of this chapter. Only 6 infants in this group gave a d_{max} above the minimum displacement, 0.16 deg, and it was not possible to calculate a median. However at 40 msec interval, only two of these infants showed a d_{max} of less than 0.16 deg. A significant majority of the infants whose results could be compared showed a larger d_{max} at 40 msec interval (10/11; $P < 0.05$, sign test). No such difference was apparent when the results were expressed as velocities. Here, eight infants could be compared; four showed a larger v_{max} at 20 msec interval, and four at 40 msec. These results, shown in Fig 4.3(a), suggest that the performance of 8-11-week-olds is characterised by a velocity limit rather than a displacement limit.

Clearer and quite different results were obtained from the older group [Fig

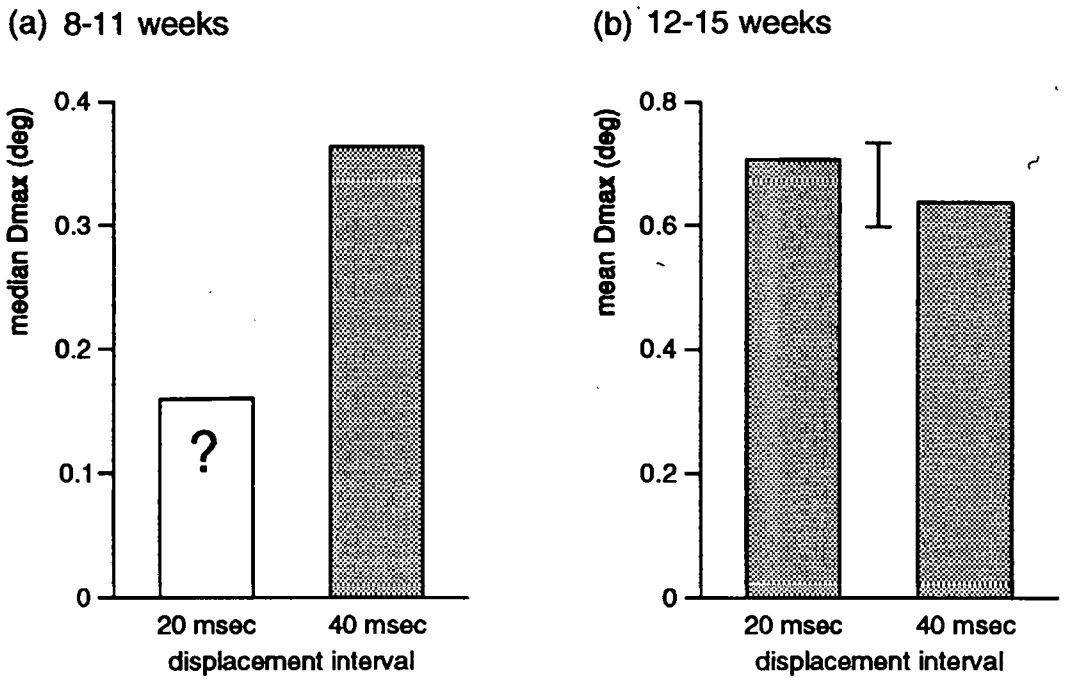

Fig 4.3 Comparison of d_{max} at displacement intervals of 20 and 40 msec. (a) Median d_{max} from the 8-11 week group. The 20 msec results are marked with a '?' to indicate that the median lay at some unknown point between 0 and 0.16 deg (see text). (b) Mean d_{max} from the 12-15 week group. The error bar shows the standard error of the mean of individual differences at the two intervals. Individual results are given in Table 4 of Appendix 4.

4.3(b)]. d_{max} was always greater than 0.16 deg, and there was no significant difference between the two displacement intervals ($t = 0.89$, $P > 0.4$). However when the results were expressed as velocities, v_{max} was significantly greater at 20 msec interval ($t = 2.95$, $P < 0.02$). The performance of infants aged 12 weeks and above is evidently displacement limited.

For both single and multiple displacements, adults' d_{max} does not change much when the temporal parameters of the stimulus are varied over a fairly wide range. However there is a lower limit to this range, at about 20 msec, below which d_{max} decreases approximately along a line of constant velocity (Baker & Braddick, 1985b; Nakayama & Silverman, 1984; Snowden & Braddick, 1989). The results of Fig 4.3(b) indicate that 12-15-weeks-olds have a similar lower temporal limit; this aspect of the temporal properties of motion detection appears to be quite mature by this age. Evidently this is not the case for the 8-11 week group (Fig 4.3(a)). A natural interpretation of this is that the younger infants lack motion detectors sensitive to short delays, so that d_{max} depends on detectors with larger values of ΔT which, with short

displacement intervals, can only respond to every second (or third etc) displacement.

It appears then that one process involved in the development of sensitivity to high velocities is an early maturation of the temporal properties of motion mechanisms which is largely complete by around 12 weeks. This is reminiscent of the rapid development of sensitivity to high temporal frequencies (Regal, 1981; Moskowitz & Sokol, 1980; Hartmann & Banks, 1992), which, at least at low spatial frequencies, is also adult-like by about 3 months. The development of d_{max} continues well beyond this age (Fig 4.1), which points to a second process involving maturation of the spatial properties of motion mechanisms. The most obvious candidate here is the emergence of mechanisms with larger spans (ΔS). However as was pointed out in the introduction, mechanisms with sufficiently large spans are necessary but not sufficient to explain d_{max}; interactions between mechanisms are also important. The possible role of these factors in the development of d_{max} is discussed below.

Coherent/incoherent and direction discrimination compared

Although the development of d_{max} for coherent vs incoherent motion (Fig 3.2) and for opposite directions (Fig 4.1) have similar patterns, absolute values of d_{max} are quite different. This is illustrated in Fig 4.4, which replots some of the data from Figs 3.2 & 4.1 for 3 comparable age groups (including adults). d_{max} is plotted on a logarithmic scale, and the curves are approximately parallel; throughout the age range d_{max} for coherent vs incoherent motion is around three times greater than d_{max} for opposite directions. This constant ratio suggests that there may be some common factor underlying the development of d_{max} for these two tasks. On the other hand discrimination of coherent from incoherent motion is evidently possible for displacements above the upper limit for direction discrimination, which implies that, as suggested on theoretical grounds in Chapter 3, directional mechanisms are not involved in the former task, whereas they are clearly necessary for the latter. However this point is not entirely straightforward, and clarification requires a closer look at the effect of task on adults' d_{max}.

Two distinct paradigms have been used in adult experiments. Braddick (1974) first measured d_{max} for segregation; subjects had to report the orientation of a rectangular region of coherently displaced random dots surrounded by incoherently

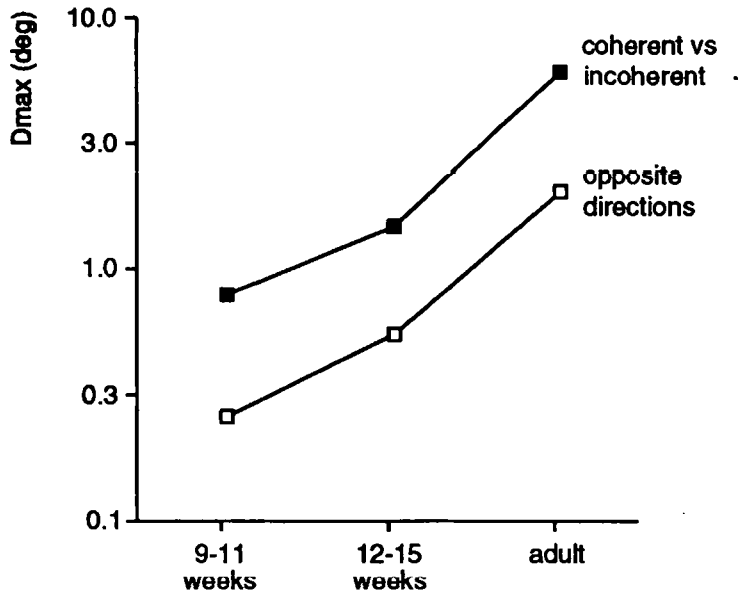

Fig 4.4 This figure compares the development of d_{max} for coherent vs incoherent motion (filled symbols) with that for discrimination of opposite directions (open symbols). Median values of d_{max} are plotted on a logarithmic scale. The data come from the experiments whose results are illustrated in Fig 3.2 (the main experiment of chapter 3) and Fig 4.1(the first experiment of the present chapter); the results of all infants from these two experiments who fell into the two age groups (9-11 and 12-15 weeks) are included.

moving dots. Since then the majority of studies have used absolute direction discrimination tasks, in which the subject makes a forced choice between two opposite directions of motion, though segregation tasks have also been used occasionally. In direct comparisons, absolute direction discrimination gives higher values of d_{max} (Baker & Braddick, 1982b; Chang & Julesz, 1983a; Nakakyama & Silverman, 1984). The present experiments evidently involve segregation. The stimuli are most comparable to those used by Nakayama & Silverman (1984), which consisted of alternating horizontal strips of leftwards and rightwards motion. For the most part these authors measured d_{max} for the appearance of segregation in their stimulus; however in one experiment they measured it for discrimination of absolute direction in the lowest panel, and obtained values about 50% greater than for segregation. This suggests that directional mechanisms might operate at displacements above the d_{max} values reported in this chapter. Could this at least partly account for the higher values of d_{max} for coherent vs incoherent motion; might directional mechanisms after all be involved in this discrimination? Clearly even if this is so, it leaves unanswered the question of why

d_{max} is so high for this task, since it too involves segregation. Before discussing this, it will be useful to directly compare adults' d_{max} for the two tasks used so far with that for absolute direction discrimination in the same stimuli.

For absolute direction discrimination, targets were displayed on both sides against an incoherently-moving background. They moved coherently in the same direction, without direction reversals, and the subject had to decide whether they moved up or down. In the previous experiments any temporal integration involved in determining direction was presumably limited to half a period of the motion's oscillation; trial duration was therefore set to this value (0.24 sec). For direct comparison, the coherent vs incoherent and opposite direction segregation tasks used previously were repeated, this time with a trial duration of 0.24 sec, so that again there were no direction reversals.

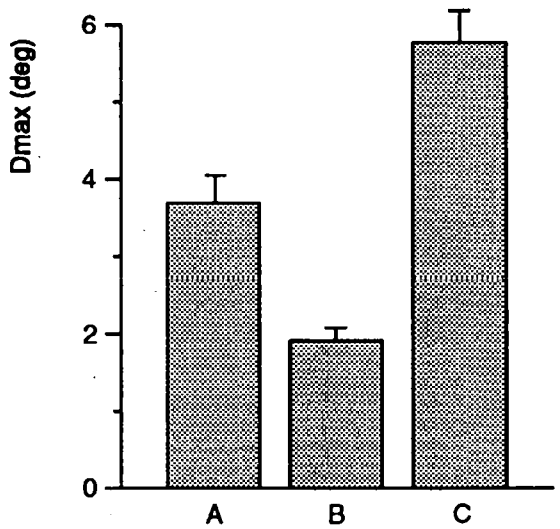

Fig 4.5 Mean (+1 standard error) d_{max} from three adult subjects. (A) Absolute direction discrimination. (B) Discrimination of opposite directions (segregation). (C) Discrimination of coherent from incoherent motion. Individual results are shown in Table 5 of Appendix 4.

The results are illustrated in Fig 4.5. d_{max} was clearly greater for absolute direction discrimination (A) than for segregation of opposite directions (B), which agrees with the comparisons cited above. The largest values of d_{max} were found for segregation of coherent from incoherent motion (C); evidently this discrimination is possible at displacements above those for which motion direction can be determined, and it appears that after all non-directional mechanisms are involved. There is an odd discrepancy here with the results of Baker & Braddick (1982b) and Chang & Julesz

(1983a). Both of these studies found that d_{max} for segregation, with an incoherent background, was less than for absolute direction. A possible explanation is that the non-directional mechanisms which appear to support this segregation in the present experiments require multiple displacements to reach maximum sensitivity, and are less effective than directional mechanisms with the single displacements used in these other studies (see Appendix 3). Alternatively the segregation supported by these mechanisms, while adequate for the left-right location task used here, may be too imprecise for the figural discrimination tasks employed in the other studies.

The finding that absolute direction d_{max} was twice that for directional segregation might suggest that in the latter, discrimination depends on direct detection of the relative motion at the boundary between adjacent regions. These relative displacements are twice the absolute displacement of each region. However Baker & Braddick (1982a) have shown that segregation depends on absolute displacement, which implies that the motion is detected by mechanisms operating separately in each region, whose outputs are then combined in order to segregate the image. The appearance of the segregated stimuli in the present experiments suggests a similar scheme; near d_{max} the regions no longer appear sharply segmented, but instead consist of a narrower strip of (relatively) coherent motion, with strips of incoherent motion separating neighbouring regions. This incidentally underlines the fact that segmentation with well-defined borders is not necessary for discrimination in these tasks.

The absolute direction discrimination results can be compared with previously published measures of d_{max} using this task. Stimulus eccentricity is one of the most important determinants of d_{max}. This has been explored extensively by Baker & Braddick (1985a), who obtained values of about 1.5 deg for a single displacement at an eccentricity of 10 deg. Extrapolating their results suggests a value of around 2.2 deg at 15 deg (the eccentricity of the outer edge of the target in the present experiments). The sequential recruitment that is found with multiple displacements, as used here, will increase this by a factor of 1.5 (Nakayama & Silverman, 1984; Snowden & Braddick, 1989) to 3.3 deg. Finally a further, perhaps modest, increase is likely as a result of the much larger rdp elements used in the present experiments (Morgan, 1992). Despite the obvious uncertainties of translating between the conditions of Baker & Braddick's experiment and the present one, the end result is quite compatible with the value of 3.7

deg found here.

Like adults, infants show a d_{max} for coherent vs incoherent motion which is about three times that for discrimination (segregation) of opposite directions. This implies that the apparently parallel development of d_{max} for the two tasks (Fig 4.4) is not simply a result of the same visual mechanisms being involved. Is it a coincidence, or does it reflect a less specific common factor? In the previous chapter it was suggested that the development of d_{max} for coherent vs incoherent motion might reflect the emergence of mechanisms with larger receptive fields. With the added assumption that the span, ΔS, of a directional mechanism is related to its overall receptive field size, a similar explanation might apply to the development of d_{max} for direction discrimination. There is both psychophysical (van der Grind et al, 1986; Cleary & Braddick, 1990a) and neurophysiological (Baker & Cynader, 1986; Mikami et al, 1986) evidence that ΔS scales with receptive field size in the mature visual system, and it is quite plausible that the same is true during development.

This scheme implies an increase in sensitivity that is specific to (or at least greatest for) large displacements. However the results do not rule out the alternative - that the improvement in d_{max} results from a uniform increase in sensitivity at all displacements, such as might arise from greater efficiency of global processes involved in disambiguating local motion signals. This issue will be taken up again in Chapter 6, which describes experiments on motion sensitivity at intermediate displacements. Meanwhile, the next chapter returns to another intriguing question raised by the results of this chapter: are infants younger than 8 weeks sensitive to the direction of motion?

Conclusions

The main finding of this chapter was that d_{max} (and thus v_{max}) for discrimination of opposite directions increases substantially during development. Thus this chapter provides direct behavioural confirmation of the hypothesis, suggested in Chapter 1 on the basis of indirect evidence from VEP, OKN and smooth pursuit studies, that directional motion processing (and thus presumably cortical directional selectivity) emerges first at relatively low velocities, spreading to higher velocities with age. d_{max} was not affected by stimulus contrast, which indicates that its development is not simply a result of improving contrast sensitivity, but represents specific changes in the

population of directional motion detectors. The results of changing the displacement interval suggest two distinct (but quite possibly overlapping) processes underlying the increase in d_{max}: a rapid maturation of the temporal properties of directional mechanisms (ie the emergence of mechanisms with small values of ΔT), which at least with the stimuli used here is largely complete by about 3 months; and a more prolonged development of their spatial properties. Two possibilities for the latter process were identified: a specific improvement in sensitivity to large displacements, such as might arise from the emergence of detectors with large values of ΔS, or a uniform improvement in sensitivity across all displacements. These two possibilities are not mutually exclusive.

5 The onset of directionality

In the introduction, a number of studies were cited which show that the lower velocity threshold (v_{min}) for detection of motion against a static background decreases with age. It was argued that this threshold provides a lower bound for v_{min} (and thus presumably d_{min}) for direction discrimination, and that the latter is also likely to decrease with age. At the same time, d_{max} increases with age. The picture which emerges, of a velocity range over which infants are sensitive to direction that expands during development, raises the possibility that very young infants (ie those less than 8 weeks) may be unable to discriminate direction at any velocity. The present chapter explores this possibility. To set the scene, the first experiment looks at the development of d_{min} in slightly older infants.

The development of d_{min} for direction discrimination

The measurement of d_{min} requires much smaller displacements than minimum of 0.16 deg available in the previous experiments. These were achieved by using sub-pixel positioning, which is described in Appendix 1. Horizontal motion was chosen for the experiments of this chapter; as before, the stimulus was displayed on a grid of 640 by 256 pixels, which meant that the pixels were half as wide as they were high, so that horizontal motion gave the smallest possible displacements, and the least visible sampling artifacts with sub-pixel positioning (these are described in Appendix 1). Fig 5.1 shows details of the stimulus. The uniformly illuminated central gap was introduced to eliminate vertical borders between regions with opposite directions of motion; the accretion and deletion of texture at such borders might otherwise provide a non-directional cue to the target's location. The other major change was the use of rdps with larger elements; the stimulus was designed to be used with very young infants, and larger elements result in more energy concentrated at the low spatial frequencies to which they are most sensitive.

This experiment measured d_{min} and d_{max} in twelve 10-week-old and nine 13-week-old infants. Only eight of the 10-week and seven of the 13-week group managed both; for the remaining five infants, only d_{min} was measured. Thresholds were

Fig 5.1 The stimulus used to measure d_{min} for direction discrimination. The overall size was the same as in the previous experiments (48 x 39 deg). The central gap was 10.2 deg wide (hence the inner edge of the target was 5.1 deg from the midline), and its luminance was equal to the mean luminance of the rdp. Type 1 rdps with an element size of 0.64 deg were used. The target was 12.6 deg high. Motion was along the horizontal axis; with sub-pixel positioning, displacement size could be varied in steps of 0.0053 deg. As in previous experiments, the displacement interval was 20 msec, and the direction of motion reversed every 240 msec.

measured with the 2-up/1-down procedure described in Appendix 2. Staircases started at 0.21 deg for d_{min} and 0.15 deg for d_{max}, and displacement was varied in steps of one quarter of an octave. The results (Fig 5.2) showed the expected pattern; the older infants gave a larger d_{max} and a smaller d_{min}, and for both the differences between the two age groups were significant (d_{max}: $t = 2.76$, $P < 0.02$; d_{min}: $t = 7.17$, $P < 0.001$). d_{max} was greater than d_{min} in all of the infants who were tested for both. Interestingly d_{max} values were quite similar to those obtained from infants of the same ages in the first experiment of the previous chapter (these are indicated in Fig 5.2). The changes made to the stimulus appear to have had little effect.

There is obviously a great deal more to be learnt about the development of d_{min}, such as its time course over a longer period; its exact relationship to v_{min} for the motion vs static discrimination; and the factors underlying it, which could be explored in experiments analogous to those of chapter 4. However these questions are not pursued in the present work. The focus of this chapter is on the implications of the expanding

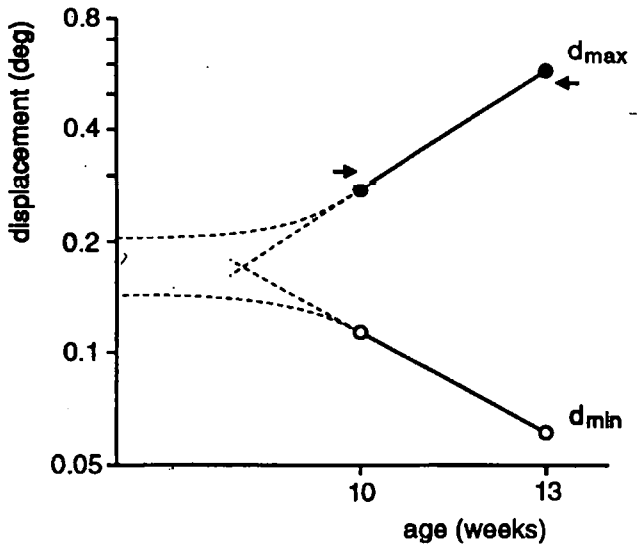

Fig 5.2 The development of d_{min} and d_{max} between 10 and 13 weeks. Mean thresholds are plotted on a logarithmic scale (but were calculated prior to the log transform) to allow both to be plotted together without unduly compressing the change in d_{min}. Note that the backwards extrapolations from the data (broken lines) are purely illustrative. The arrows show the values of d_{max} obtained from infants of the same ages in the first experiment of Chapter 4. Individual results are given in Table 6 of Appendix 4.

gap between d_{min} and d_{max} for the performance of younger infants. The aim is to distinguish between the alternatives which are illustrated by the two ways shown in Fig 5.2 of extrapolating back from the data to younger ages. In the first, d_{max} meets d_{min}, so that there is some age before which infants are not sensitive to direction for any displacement size (and thus velocity), while in the second the thresholds do not meet; from birth, infants can discriminate direction, though only over a narrow range of displacements.

Motion processing in one-month-olds

Preferential looking experiments

The exploration of motion processing in younger infants started with preferential looking experiments using the stimulus of Fig 5.1. The interval between direction reversals was increased to 0.48 sec; this value was chosen as a plausible compromise between the possibility of improved sensitivity to the direction of motion, and the likelihood of significant OKN (which could result in a spurious cue to the target's location - see Chapter 2), with longer intervals. In other respects the stimulus used to

test direction discrimination was unchanged. However, since one predicted outcome is a failure of direction discrimination, ie chance performance with this task, a control condition which results in above chance performance is clearly desirable. An obvious candidate is discrimination of a coherently moving target from a static background, which should be possible at all ages. An alternative is the discrimination of coherent from incoherent motion; previous experiments (and the analysis in Appendix 3) suggests that even infants who are insensitive to direction may well be capable of this. In addition to the direction discrimination task, both of these control conditions were used by making the appropriate changes to the behaviour of the background regions of the stimulus in Fig 5.1. All three conditions used the longer (0.48 sec) interval between reversals.

Attempts to use a staircase to measure direction discrimination d_{min} and d_{max} in very young infants seem doomed to failure; even if they exist, they are likely to be so close together that each will interfere with the staircase designed to measure the other. Instead the method of constant stimuli was used. Between 10 and 20 trials were gathered at each of five displacement levels separated by 1 octave and covering the range 0.027-0.43 deg. During testing the trials cycled through the five levels, so that for individual infants the number of trials was the same at all levels. In the first experiment, a total of fifteen 3-6-week-olds gave usable results, ie a minimum of 10 trials at each level in at least one condition. For the first 7 infants only direction discrimination was tested; the control conditions were only introduced when the overall low performance in the direction task started to become apparent. After this, an attempt was made to test each subject with all three conditions in a roughly counterbalanced order, but this was only successful with one infant. A further five infants managed two conditions each and two infants managed one. Overall, 11 infants gave direction discrimination results, 5 coherent vs static, and 6 coherent vs incoherent.

Fig 5.3 shows the individual results for the direction discrimination task. They are clearly clustered around 50% performance. Of the 55 data points shown, 4 are greater than expected from chance (using the one-tailed criterion of binomial $P < 0.05$), and 3 are below chance (same criterion). These 7 points are scattered across all displacements, and the overall incidence of 12.7% is close to the expected two-tailed rate of 10%. Of course this analysis is not strictly valid, since the data points are not

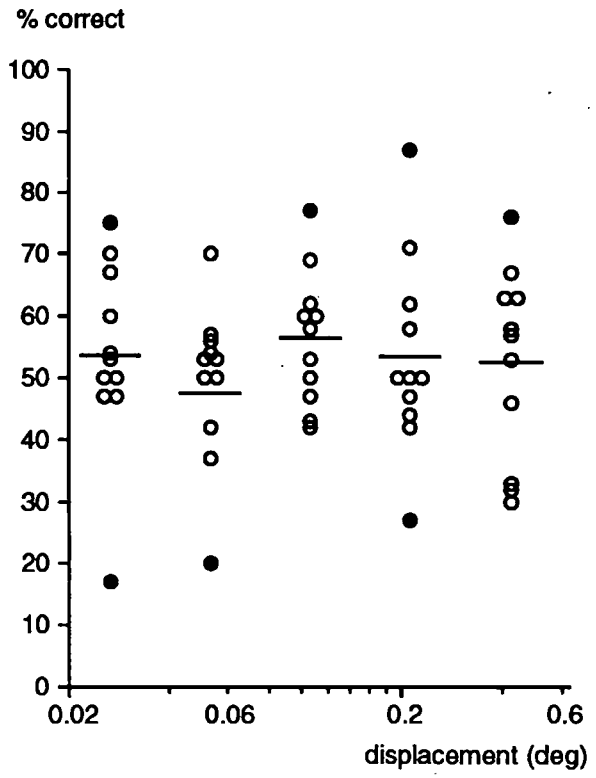

Fig 5.3 Direction discrimination FPL results from the first group of 3-6-week-olds. Each point shows the performance of a single infant as percent correct (ie percent preference for the target) out of 10-20 trials. Note that each infant contributed a point to each of the five displacement levels, though to avoid clutter no attempt has been made to link individual results across displacements. The filled symbols denote a performance that was either significantly above or significantly below chance (ie 50% correct), each based on a one-tailed binomial $P < 0.05$. The short horizontal lines show mean performance of the group at each displacement.

entirely independent (each group of 5 points comes from a single infant). Nevertheless it is clear that the individual results show little evidence for direction discrimination. The same is true for the group results - ie the mean values of percent correct at each displacement, which are shown in Fig 5.3 and replotted in Fig 5.4 (circles). As a group, the infants did not perform significantly above chance at any displacement.

Group results for the two control conditions are also shown in Fig 5.4. These gave a very different picture. The coherent vs incoherent task produced a perfomance that was well above chance at all displacements; for the coherent vs static case, the chance performance at small displacements increased to significantly above chance at the two highest levels. These results make it clear that the poor direction discrimination performance shown by the infants is specific to that task. However the usefulness of the

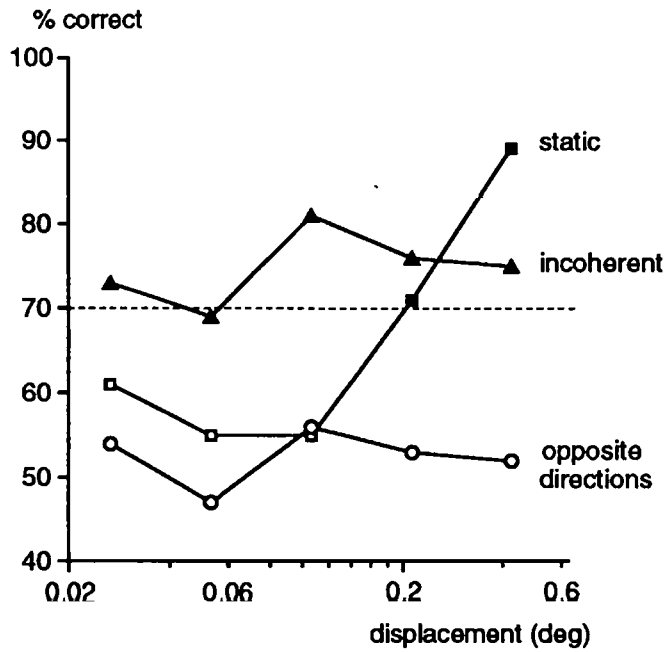

Fig 5.4 Mean FPL performance of the first 3-6-week group for all three conditions. Results plotted with filled symbols were significantly different from 50% (two-tailed t-test, $P < 0.05$), while those with open symbols were not. Individual results are shown in Table 7 of Appendix 4.

control conditions goes further than this. The coherent vs static data in Fig 5.4 show a clear threshold at about 0.2 deg; as argued above, this should provide a lower bound for the displacement range over which direction discrimination is possible (if at all). In addition, previous results have shown that d_{max} for the coherent vs incoherent task should give an upper bound of this range (see Fig 4.4 - note that the data plotted there indicate that this is unlikely to be the *least* upper bound). This argument reveals a flaw in the present experiment - the displacements used do not extend up to d_{max} for the coherent vs incoherent task.

The next experiment was a repeat of the previous one, but with a different range of displacements and a different group of 3-6-week-olds. Direction discrimination was tested at four displacements, separated by one octave, in the range 0.11-0.85 deg. For the coherent vs incoherent task a fifth level was added to extend the range to 1.7 deg. The coherent vs static condition was not used. Direction discrimination data was obtained from ten infants, and five of these also provided coherent vs incoherent results. The group results are plotted in Fig 5.5. This time the displacement range was sufficient for performance in the coherent vs incoherent condition to fall to chance. Despite this, there was again no evidence in the group data of direction discrimination

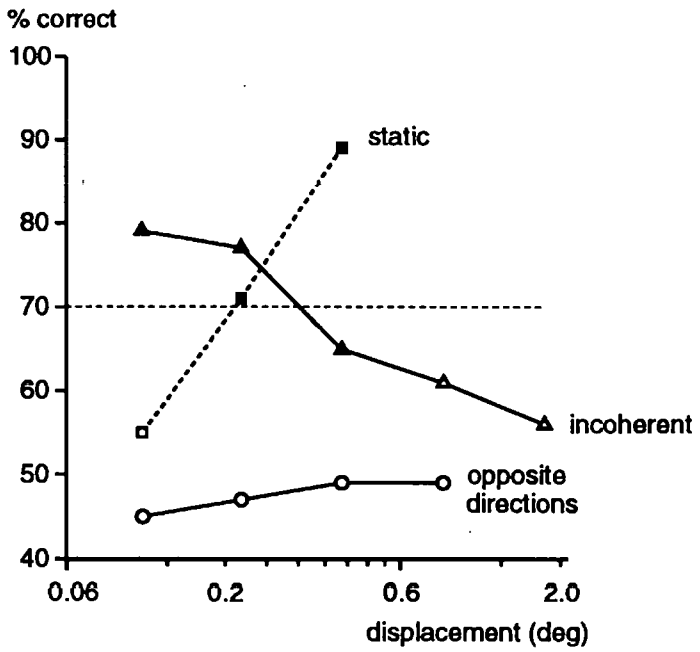

Fig 5.5 Mean FPL results from the second group of 3-6-week-olds. Note that these infants were not tested with the static condition; the results for this condition were from the first group, and are shown again here to illustrate the typical range of displacements for which infants of this age give above chance performance in both control conditions. Individual results are shown in Table 8 of Appendix 4.

at any of the displacement levels. The same was true of the individual data; only two of the 40 data points were significantly different from chance.

The obvious conclusion from these experiment is that if 1-month-olds have any sensitivity to direction of motion, it is only over a range of displacements that is substantially less than one octave wide, and thus falls through the gaps between the displacements tested[8]. If this is the case then quite small variations in the location of the range in different infants could result in no overlap, and this would make it very hard to track down. However there is another possibility. It may be that the infants are sensitive to direction over a reasonable range of displacements, but that this does not lead to a compelling preference for the target. Although this in turn implies some kind of deficit in direction discrimination which is not found with the control conditions, or in older infants, it is obviously worth investigating.

---

[8]If the width were close to one octave there would be a significantly larger number of above chance data points in the individual results, unless of course the upper and lower limits of the range are almost identical in different infants, and coincide with displacements used in the experiments. This seems rather unlikely.

Habituation experiments

Habituation is the best available method for exploring infants' ability to discriminate between two stimuli when they do not intrinsically prefer one of them, making it the obvious choice for further investigation of motion processing by 1-month-olds. The procedure is described in Chapter 2.

The habituation experiments explored all three of the conditions used in the FPL experiments. As before, motion was along the horizontal axis, and its direction reversed every 0.48 sec. During the test phase the direction discrimination display, which is illustrated in Fig 5.6, was broadly similar to the FPL display. The main difference was

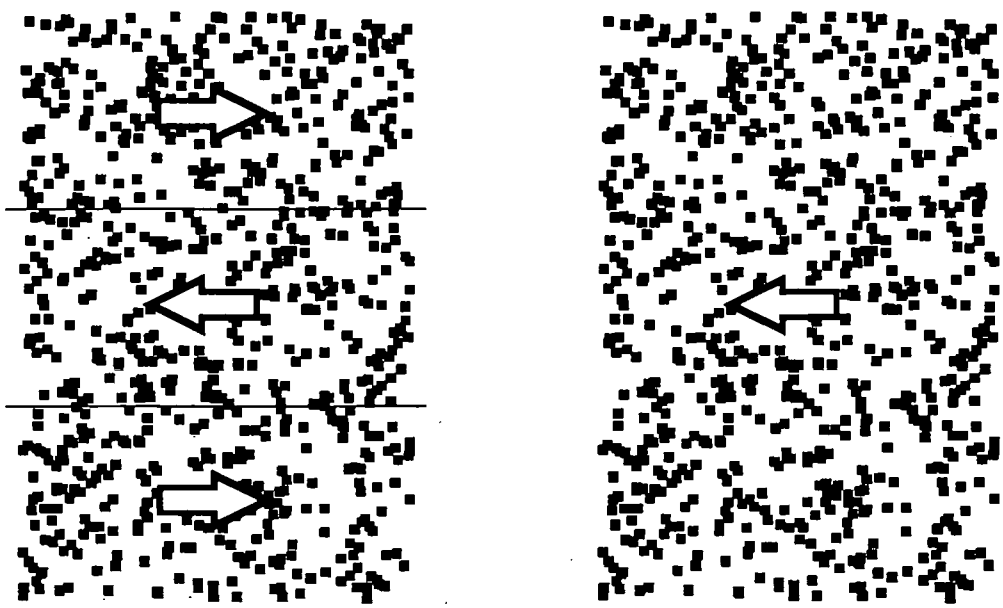

Fig 5.6 Schematic of the display during the test phase of the direction discrimination condition. The two rectangles of type 2 rdps were 19 deg wide by 30 deg high, with their inner edges separated by 10.2 deg. The three regions of the segregated stimulus (left) were each 10 deg high. During the habituation phase, the display contained a single rectangle of uniform motion, like that shown here on the right, but positioned in the centre of the screen. Note that contrast is reversed in this figure - in practice the patterns consisted of white dots on a black background.

that type 2 rdps (described in Chapter 2) were used so that several different displacement sizes could be shown simultaneously (see below). Each side consisted of 768 white elements scattered over a dark screen. The elements were confined to rectangular regions with the same width (19 deg) and eccentricity (5.1 deg) as in the

FPL display, but only 30 deg high (as opposed to 39 deg in the FPL display). The resulting reduction in the area of these rectangles meant that the density of white elements was the same in the habituation and FPL experiments; in the latter there were, on average, 1024 white elements on each side. However the elements were smaller in the habituation displays (0.48 vs 0.64 deg square), so that the mean luminance of the rdps was 75% lower. The central gap between the rdps on each side was again 10.2 deg wide, but was set to the minimum luminance of the display rather than the mean luminance of the rdps. As in the FPL experiments, the control conditions used either static or incoherently-moving dots in the backgound regions.

In the habituation trials the display consisted of a single rectangle of random dots, with the same dimensions as one of the pair of test-trial rectangles, but positioned in the centre of the screen. The rest of the screen was dark. Between both kinds of trial the entire display was dark (ie no rdps were displayed) apart from a central fixation marker; this was a 2.6 deg white square which oscillated vertically.

It is clear from the FPL experiments that the choice of displacement size is likely to be critical for 1-month-olds. Unfortunately the habituation procedure is too long-winded to allow separate tests at a number of different displacements. Instead, the infants were tested with displays containing a range of different displacements simultaneously. Type 2 rdps were chosen because they allow this. Each region of coherent motion contained a mixture of equal numbers of dots undergoing one of three displacements; for adult observers this resulted in the appearance of three superimposed transparent planes drifting at different speeds. The displacement size of individual dots did not vary and, of course, within each region all dots moved in the same direction. The displacements were 0.16, 0.24 and 0.32 deg. They were chosen to cover the low end of the range giving above chance performance in the two FPL control conditions (Fig 5.5). The high end of this range was avoided because in all older subjects its upper limit (d_{max} for coherent vs incoherent motion) is three times the upper limit for direction discrimination (Fig 4.4).

The test phase of the habituation procedure is a form of preferential looking in which preference is determined from the relative amount of time spent looking at each of the stimuli in the course of two 20 sec trials. With the full habituation procedure, the aim is to induce a preference for one stimulus by first habituating the infant to the

other. However, it seemed possible that a measure of preference based on looking time might be more sensitive than the one used in the FPL experiments (generally, the direction of first fixation), and might reveal an intrinsic preference without prior habituation. The first four infants (aged 3-6 weeks) were given the test trials without habituation. Only direction discrimination was examined. Each infant was given three sets of two 20-sec test trials, with short breaks between sets. They showed no sign of a preference, spending on average 50.1% of the time on the motion contrast stimulus (ie the side with the target) and 49.9% on the uniform motion. Despite the small number of subjects it was clear that this approach was not going to give robust evidence for an intrinsic preference, and it was promptly dropped in favour of the full habituation procedure.

For the direction discrimination task, the infants were habituated to uniform motion (ie the right side of Fig 5.6), so that in the test phase the novel stimulus was always the segregated one (left side of Fig 5.6). The alternative sequence, in which the uniform motion is the novel stimulus, could also have been used, but in this case any intrinsic preference for the segregated stimulus could undermine the effect of habituation. Clearly if there is any intrinsic preference it is very weak, but given the behaviour of older infants it is most likely to be in favour of the segregated stimulus. On balance it seemed that habituating to uniform motion, thus allowing habituation and preference to combine forces, was most likely to reveal clear evidence of direction discrimination. With static and incoherent backgrounds 1-month-olds do prefer the segregated stimulus. For these conditions, the test trials were not preceded by habituation; it was expected that the preference would show up without it. This meant that most infants could be tested under all three conditions in a single session. Direction discrimination (full habituation) was always tested first, and the order of the other two conditions was counterbalanced across subjects.

Each subject's results were expressed as the proportion of the total looking time, combined across both test trials, that the infant spent looking at the segregated stimulus. Hence a value of 50% indicates equal time spent on each stimulus, while larger values imply a preference for the segregated stimulus (though it should be emphasised that individual results have no statistical significance - evidence for discrimination depends on a consistent preference across a group of infants).

A group of fifteen 3-5-week-old infants were the first to be tested (mean age was 4.8 weeks - note this is a slightly younger group than the 3-6-week-olds tested in the FPL experiments). Their results are plotted in Figs 5.7 & 5.8 as average values of percent preference for the segregated stimulus (see above). In Fig 5.7, the direction

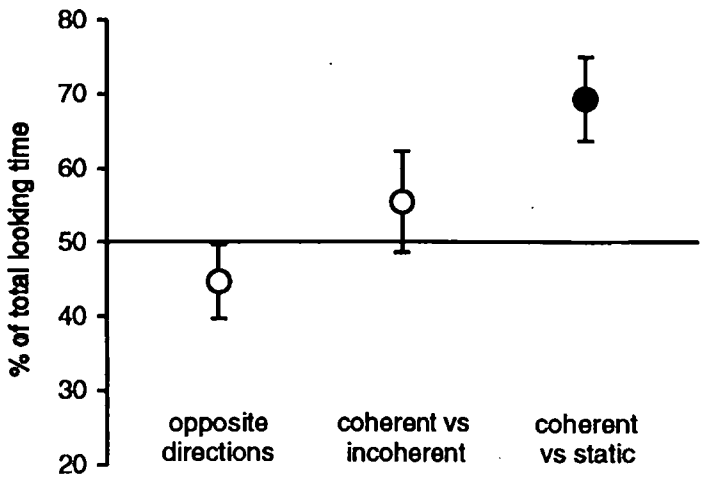

Fig 5.7 Results of the habituation experiment in 3-5-week-olds, plotted as mean values (± 1 standard error) of the percent of total looking time that the infants spent looking at the segregated stimulus over both test trials. The direction discrimination result ('opposite directions') is from all 15 infants, and the test trials were preceded by habituation to the uniform stimulus. For the two control conditions there was no prior habituation, and the results are from the first 10 infants only. In this and the following figures, results that were significantly different from 50% (two-tailed t-test, $P < 0.05$) are plotted with filled symbols, while open symbols are used for results that were not significant. Individual results are shown in Table 9 of Appendix 4.

discrimination result is from all 15 infants. It was not significantly different from 50% ($t = 1.14$, $P > 0.2$, two-tailed). Despite the full habituation procedure, these infants gave no evidence of direction discrimination. The control condition results in Fig 5.7 came from first 10 infants only, two of whom did not give coherent vs incoherent data; as expected, they showed a clear preference for the segregated stimulus in the coherent vs static condition ($t = 3.5$, $P < 0.01$). Surprisingly, however, this was not the case for the coherent vs incoherent condition ($t = 0.695$, $P > 0.4$). In the light of this, the protocol was changed for the last 5 infants. The coherent vs static condition was dropped. As before, the first condition was direction discrimination with full habituation. This was followed by the coherent vs incoherent condition, only this time the infants were first habituated to incoherent motion. Fig 5.8 gives the results; after habituation to

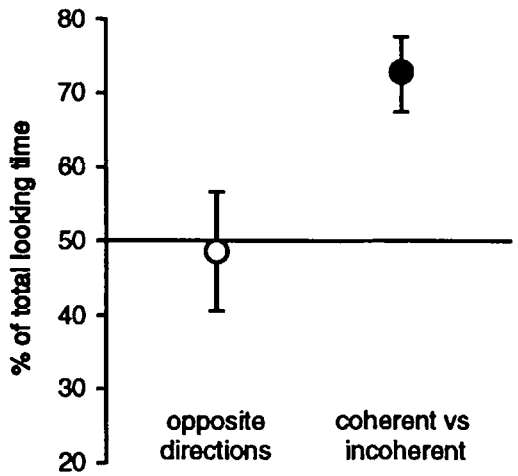

Fig 5.8 Habituation results from the last five infants of the 3-5-week group. In both conditions (direction discrimination and coherent vs incoherent), test trials were preceded by habituation to the uniform stimulus. Note that the direction discrimination data for these 5 infants, whose mean is plotted here, also contributed to the result shown in Fig 5.7. Individual results are shown in Table 9 of Appendix 4.

incoherent motion the infants showed a strong preference for the segregated stimulus (t = 4.45, $P < 0.02$). Fig 5.8 also shows the direction discrimination result for these 5 infants, which was again not significantly different from 50% ($t = 0.39$, $P > 0.5$); note that the data from these infants also contributed to the direction discrimination result plotted in Fig 5.7.

The finding that habituation was required to demonstrate discrimination of coherent from incoherent motion suggests that measurement of relative looking time over two trials is a less sensitive index of intrinsic preference than the direction of first fixation over 10 or more trials, as used in the FPL experiments. It also demonstrates that these very young infants will show habituation recovery to changes in the dynamic behaviour of the rdps.

The results of the habituation and FPL experiments point to the same conclusion: 1-month-olds only fail to discriminate between the segregated and uniform stimuli in the direction discrimination task, which suggests that they are unable to distinguish between the opposite directions of motion in the segregated stimulus. This leads naturally to the question of when infants first show this ability. From the results of Chapter 4 (Fig 4.1) it is clear that at least some 8-9-week-olds have it, but this still

leaves a gap between 5 and 8 weeks. The next experiment was designed to fill it.

Nine 6-8-week-olds (mean age 7.5 weeks) were tested in a habituation experiment which followed the original protocol: direction discrimination with full habituation first, followed by test-trials only for the two controls. One infant did only the direction discrimination condition, while the rest managed all three. The results are

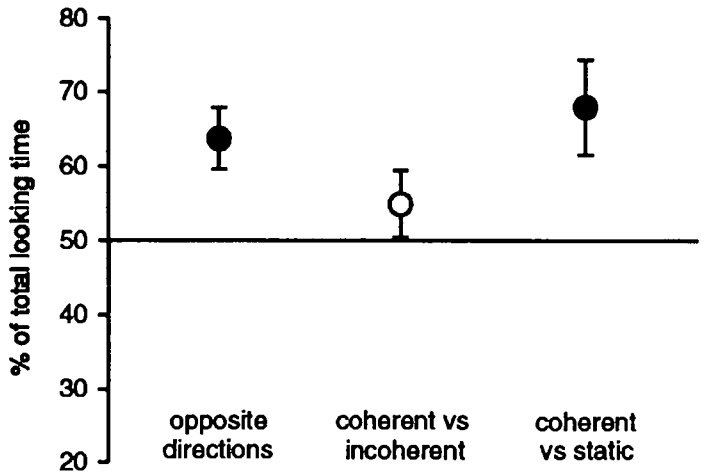

Fig 5.9 Results of the habituation experiment with the 6-8-week group. The protocol was the same as in Fig 5.7. Individual results are given in Table 10 of Appendix 4.

illustrated in Fig 5.9. After habitutuation to uniform motion in the direction discrimination condition, these older infants showed a clear preference for the novel, segregated stimulus (t = 3.364, $P < 0.01$). The control condition results followed the pattern found in 3-5-week-olds; a significant preference for the segregated stimulus for the coherent vs static discrimination (t = 2.62, $P < 0.05$) but, interestingly, not for coherent vs incoherent motion (t = 1.02, $P > 0.3$); no doubt the full habituation procedure would give a positive result for this condition, as it did with the younger group, though this was not attempted.

These habituation results are quite striking. The clear evidence for direction discrimination in the older group adds considerable weight to the negative finding in infants just 3 weeks (on average) younger. The results seem to pinpoint the onset of directionally-selective responses to within about 3 weeks, at 5-6 weeks of age. However there is another possibility. In these experiments discrimination may depend on the ability to use directional information for segregation, and this ability may develop later than the underlying directional mechanisms.

Discrimination of absolute direction (eg leftwards vs rightwards motion) should provide the most unambiguous evidence for directional selectivity. The next experiment examined this discrimination, again using habituation. Certain problems were anticipated with this experiment; the continuous unidirectional motion of the stimuli is likely to generate significant OKN which could make it impossible for the observer to remain ignorant about which stimulus the infant was viewing. Moreover the OKN would make it hard to interpret a positive result; is discrimination based on cortical directional responses, or on feedback from the eye movements, in which case cortical directionality may be unnecessary? In practice, only short bursts of OKN were seen, and it was much less prevalent than expected, particularly in the younger infants. When present in the test trials it did not cause any ambiguity about which side of the display the infant was fixating, and it was surprisingly hard to decide whether or not it was in the same direction as any OKN seen during the habituation trials.

The stimuli were similar to those of the previous experiment, though of course the dots moved in one direction only, without reversals. Infants were habituated to one of the directions (left or right), and then tested with leftwards motion on one side of the display, and rightwards on the other (as before the sides were swapped for the second test trial). Discrimination was tested for two kinds of motion: the simultaneous mixture of three displacement sizes (0.16, 0.24 & 0.32 deg) used before, and a single displacement size (0.24 deg). In addition, both directions of motion were used as habituation stimuli. Of the four possible conditions, two were attempted with each infant; in the second run both the type of motion, and the direction of motion in the habituation phase were changed. Results were obtained from 19 3-5-week-olds (mean age 4.5 weeks), with 12 completing two runs while the rest managed only one; and 21 6-8-week-olds (mean 7.6 weeks), 9 of whom completed two runs.

The results were combined across the different habituation directions, but kept separate for the different type of motion. They are shown in Fig 5.10. Neither age group showed any evidence that they could discriminate between leftwards and rightwards motion. For the 3-5-week-olds this result agrees with the previous experiments and supports the idea that they lack directional mechanisms. However with 6-8-week-olds the contrast between the present negative result and the the positive result of the previous experiment seems quite paradoxical, particularly since the absolute direction

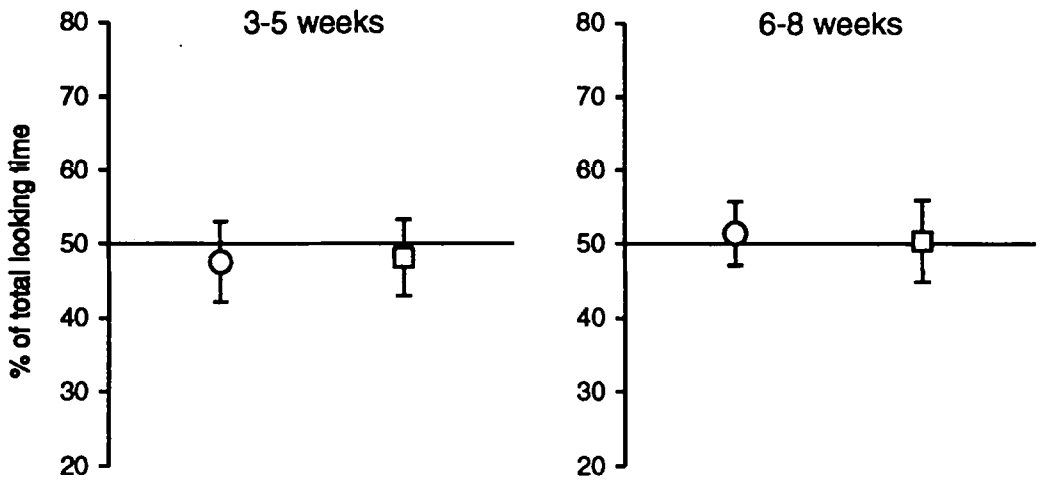

Fig 5.10 Results of the habituation experiment on absolute direction discrimination. Circles: single displacement size (0.24 deg). Squares: three simultaneous displacement sizes (0.16, 0.24, 0.32 deg). Individual results are given in Table 11 of Appendix 4.

task was chosen because it seemed likely that sensitivity to absolute direction might be a precondition for direction-based segregation, and might therefore provide the earliest evidence for directionality. A mundane explanation is that the infants were rather immature; if directionality emerges at about 5-6 weeks, then there may be quite a good chance of selecting a small group of 6-8-week-olds that has a high proportion of infants who lack directionality. There is also a more interesting explanation. It was argued above that feedback from eye movements might allow infants to discriminate absolute direction even if they lack cortical directionality. This argument can be turned on its head. For adults, these stimuli have a well-defined and stable direction and speed which is essentially unaffected by the presence or absence of eye movements. Directionally-selective mechanisms are obviously needed for this. However by themselves these only provide information about motion in the retinal image, and eye movements can transform a given physical motion into quite arbitrary retinal motions. A stable percept also needs feedback about eye movements; without this, both the speed and to a lesser extent the direction of the stimuli would appear quite unstable, which might well disrupt absolute direction discrimination. In the segregated vs uniform task the direction reversals eliminate large tracking eye movements. Hence the difference in direction between adjacent regions will be a stable feature of the retinal image, making eye movement feedback unnecessary for discrimination. In this view relative motion, as

in the segregated stimulus, should provide the earliest evidence for directionality; discrimination of absolute direction must wait until the visual system has learnt how to combine eye movement feedback with signals from directional mechanisms. The apparently paradoxical results from 6-8-week-olds suggests that they have not yet achieved this.

This argument is based on the idea that absolute direction discrimination is disrupted by eye movements that occur while the infants are viewing the stimulus. However without adequate feedback about eye movements, it will be impossible for the visual system to learn how to assign distinct and consistent labels to different physical directions of motion. This raises the possibility that although regions moving in opposite directions are registered as different, information about the nature of the difference is lost. Under these circumstances absolute direction discrimination may well be impossible even in the absence of eye movements. Unfortunately it would be difficult to test this. A related question which deserves attention, and which could be readily tested, is whether the segregated vs uniform discrimination would be disrupted by allowing tracking eye movements - ie by removing the direction reversals. It is quite possible that it would not be; although certain eye movements could eliminate direction differences in the retinal image of the segregated stimulus, there would still be marked speed differences to act as a cue for segregation.

The results of this chapter make it clear that the onset of direction discrimination, and thus by inference the emergence of directionally-selective cortical neurons, happens before two months of age. Directional-selectivity is a prominent (though perhaps not exclusive) property of the cortical systems fed by the magnocellular pathway. Other characteristic properties of this system - sensitivity to stereoscopic disparity and to high temporal frequencies - develop later, at around 2-4 months. It may be that, as suggested in Chapter 1, the earliest directional mechanisms are parvocellular, while the subsequent spread of sensitivity to higher velocities is at least partly a consequence of the later emergence of magnocellular mechanisms. However it is equally plausible that this pattern reflects the natural course of development in the magnocellular stream; there is no *a priori* reason to suppose that different characteristics of a particular pathway should all emerge at the same time. In terms of evolution, motion sensitivity may be the most primitive of all visual functions

(Horridge, 1984), in which case it is not unreasonable that it should be the first magnocellular property to emerge during development.

There is considerable evidence for close links between the development of motion processing and binocularity. The onset of cortical binocularity is correlated with the emergence of symmetrical monocular OKN (Smith, 1989; Wattam-Bell et al, 1987). Moreover abnormal binocular vision resulting from conditions such as strabismus and amblyopia is often associated with a persistence of asymmetrical OKN (Atkinson & Braddick, 1981; Smith et al, 1991). Tychsen and Lisberger (1986) found that more direct measures of cortical motion processing (smooth pursuit dynamics and velocity judgements) were abnormal in adults who lacked binocularity following strabismus in infancy. In all these cases motion processing deficits show up as directional asymmetries; in other words it appears to be directionally-selective cortical mechanisms whose development is disrupted. Tyschen and Lisberger (1986; Tychsen, 1989) have gone so far as to suggest that the normal development of binocularity might depend on the prior development of cortical directionality, and that disruption of the latter can be a primary cause of early-onset strabismus and abnormal binocular vision. The present results indicating that directionality emerges before binocularity are clearly compatible with this idea.

The failure to find evidence for directionality before 6 weeks contrasts with habituation experiments showing clear evidence for orientation selectivity in newborns (Atkinson et al, 1988; Slater et al, 1988). In these experiments newborns successfully discriminated between opposite oblique gratings, a task which is roughly analogous to the absolute direction discrimination used here. Interestingly, the ability to use orientation information for texture segregation (analogous to the segregated vs uniform motion task) appears much later (Atkinson & Braddick, 1992; Sireteanu & Rieth, 1992a,b). Development appears to take opposite courses in the two domains, which makes sense if a primary function of orientation selectivity is the analysis of isolated contours, while that of direction selectivity is segmentation of the visual scene.

Conclusions

At this point it would be nice to be able to state definitely that directionality emerges at about 7 weeks of age. The results strongly suggest this; younger infants showed no sign

of directionality in either the FPL or habituation experiments, while positive evidence for it was obtained from infants just 3 weeks (on average) older. Moreover there is close agreement between the present results and indirect evidence for cortical directionality from studies of smooth pursuit, which also emerges at around 6-8 weeks (Aslin, 1981). However it remains possible that the precise conditions necessary to demonstrate directionality in younger infants were not met. The present results do indicate a specific impairment of direction discrimination which is not found in older infants, or with the other forms of motion discrimination examined here. It seems reasonable to conclude that in day-to day experience very young infants are essentially 'direction-blind'.

6 Spatiotemporal integration in motion detection

Motion perception cannot be understood solely in terms of the properties of local detectors. In many ways the more interesting (and difficult) issue concerns the ways in which the visual system combines local measurements to produce a more global view of what is going on in the image. Two of the most fundamental of these global processes were mentioned in the introduction: integration or grouping is needed to resolve the inherent ambiguity of local motion signals and to make physically coherent moving regions of the image perceptually coherent, while an apparently conflicting process of differentiation is required to segment the image so that signals arising from physically distinct objects are dissociated (Braddick, 1993b).

This chapter describes some preliminary experiments on global aspects of motion processing in infants. They were explicitly designed to explore spatial and temporal integration; as indicated above, these processes are a necessary part of motion perception, and are therefore relevant to the results of the earlier chapters. The experiments were an extension of the previous ones, and used the same kinds of stimuli; coherently moving rdps in which adjacent regions moved in opposite directions. In order to distinguish successfully between these opposite directions, any spatial integration involved in extracting information about the direction in any one region must be largely confined to that region. In practice, of course, the extent of integration may be smaller than this, in which case reducing region size should initially have no effect on sensitivity to direction. However with further reductions visual integration will start to extend over adjacent regions and sensitivity will decline. This was the approach used to examine spatial integration; the experiments measured sensitivity to direction as a function of the height of the adjacent regions of opposite directions. Temporal integration was explored in an analogous fashion. As in previous experiments, the direction of motion reversed periodically, and sensitivity was measured as a function of the interval between reversals.

A second purpose of these experiements was to examine infants' motion sensitivity at intermediate displacement sizes, away from d_{max} or d_{min}. One way of doing this is to measures the effect on performance of degrading the motion. In type 2

rdps motion can be degraded by reducing its coherence - the percentage of dots in any one region which move coherently, while the rest are randomly repositioned from frame to frame (ie they move incoherently). Coherence thresholds provide a measure of the visual system's ability to extract motion signals from noise (van Doorn & Koendrink, 1982a,b; Newsome & Pare, 1988; Snowden & Braddick, 1989a), and were used here to assess sensitivity to the difference in directions between adjacent regions of the motion contrast stimulus. Thresholds were measured at a fixed displacement size of 0.16 deg in FPL experiments using the 2-up/1-down staircase. Staircases started at 100% coherence, and step size was ¼ octave. Each side of the display showed a 19 deg wide by 30 deg high rectangle of type 2 rdps, with a 10.2 deg wide gap between them. Motion was horizontal, and on the target side was segregated into alternating horizontal bands of opposite directions, while on the non-target side it was uniform; all the coherent dots move in the same direction. The dots were 0.32 deg square, and there were 1056 of them on each side. In any given trial, coherence was the same on both sides.

The infant subjects were 3-month-olds (11-15 weeks). Spatial and temporal integration were examined in separate experiments which used different groups of infants. In each experiment, the parameter that was not being explored was fixed at the largest value used in the other experiment, which meant that there was one condition that was common to both. Three threshold estimates, using different temporal or spatial parameters, were attempted in each subject. At least two had to be successful for that subject's data to be included in the results. An adult subject was also tested over a wider range of stimulus parameters.

Temporal integration

The first experiment measured the effect of changing the interval between direction reversals on coherence thresholds. The spatial parameters of the stimulus were fixed; the target side was segregated into three regions, each 10 deg high, resulting in the configuration shown in Fig 5.6. The infants were tested with reversal intervals of 0.12, 0.24 and 0.48 sec. Out of the total of 15 infants, eleven gave thresholds at 0.12 sec, all fifteen at 0.24 sec and thirteen at 0.48 sec (see Table 12, Appendix 4).

Six infants (5 at 0.12 sec and 1 at 0.24 sec) failed to perform above chance at

100% coherence. These infants were assigned a threshold of >100%, which allowed median thresholds for the group to be calculated. They are plotted in Fig 6.1, along with results from the adult subject over a wider range of intervals. Overall, the infants were much less sensitive; they required 50% or more of the dots to move coherently to discriminate between the opposite directions, compared with 5-7% for the adult. The

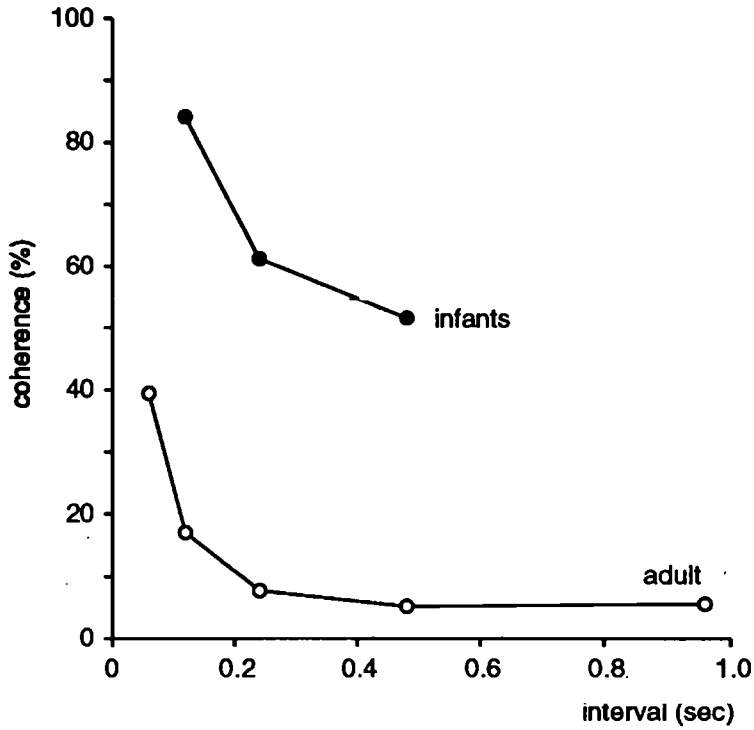

Fig 6.1 Coherence thresholds as a function of the interval between direction reversals. Note that a low threshold implies high sensitivity. The infant data show median thresholds from the 3-month group. The adult data are from a single subject; each point is the median of three threshold estimates. Individual data are given in Table 12 of Appendix 4.

adult data show a clear improvement in performance as the reversal interval increases up to 0.24 sec, but little change after that. The infants also did better at the longer intervals. The only statistics attempted on the infant data were comparisons between each possible pair of intervals, using the Wilcoxon signed-rank test; for each comparison only infants who gave both thresholds were included. The differences between 0.12 sec and the two longer intervals were both significant at $P < 0.01$ (not adjusted for multiple tests), but the difference between 0.24 and 0.48 sec was not ($P > 0.1$). While this does not rule out a real improvement in infants' performance for intervals longer than 0.24 sec, it seems clear that this will be modest compared with the improvement up to this value. The present results are compatible with the idea that

sensitivity to direction can be improved by temporal integration over a period which is similar in adults and infants (ie about 0.24 sec). However it is likely that the lower limit of integration - the shortest interval over which direction can be determined - is smaller in adults; the infants' poor performance at 0.12 sec suggests that few if any would have been able to do the task at 0.06 sec, where the adult's threshold was about 40%.

Spatial integration

Spatial integration was investigated by varying the height, and thus also the number, of the horizontal regions into which the opposite directions were segregated on the target side. In the experiments so far there have been three such regions, each 10 deg high, as illustrated in Fig 5.6. In the present experiment, region height was reduced by dividing the target side into a larger number of regions, each of the same height, and with adjacent regions moving in opposite directions. Infants were tested with heights of 2.5 deg (12 regions), 5 deg (6 regions) and 10 deg (3 regions). The last condition was the spatial configuration used in the previous experiment. For all three the interval between reversals was 0.48 sec.

In this experiment 11 infants gave thresholds at 2.5 deg height, all 12 at 5 deg, and 11 at 10 deg (Table 13, Appendix 4). A total of four staircases terminated with below chance performance at 100% coherence (two in the 2.5 deg condition, and one in each of the other two), and were assigned thresholds of >100% so that medians could be calculated. The results are shown in Fig 6.2. The infants again showed rather low sensitivity. There was no significant difference between the results of this and the previous experiment for the condition that was common to both (10 deg height and 0.48 sec reversal interval; $P > 0.4$, Mann-Witney U).

None of the pairwise comparisons on the infant data were significant, despite the apparently better performance for the 5 deg condition. The adult data (also shown in Fig 6.2) gave a similar picture; there was no clear evidence for a spatial limit to sensitivity. The reason for this (at least for the adult) became apparent during testing. With a large number of narrow regions, the opposite directions no longer appeared segregated, but instead merged to produce transparent motion. This was readily distinguished from the uniform motion on the other side of the display, which meant that the task was still possible despite the lack of segregation. The stimulus was clearly

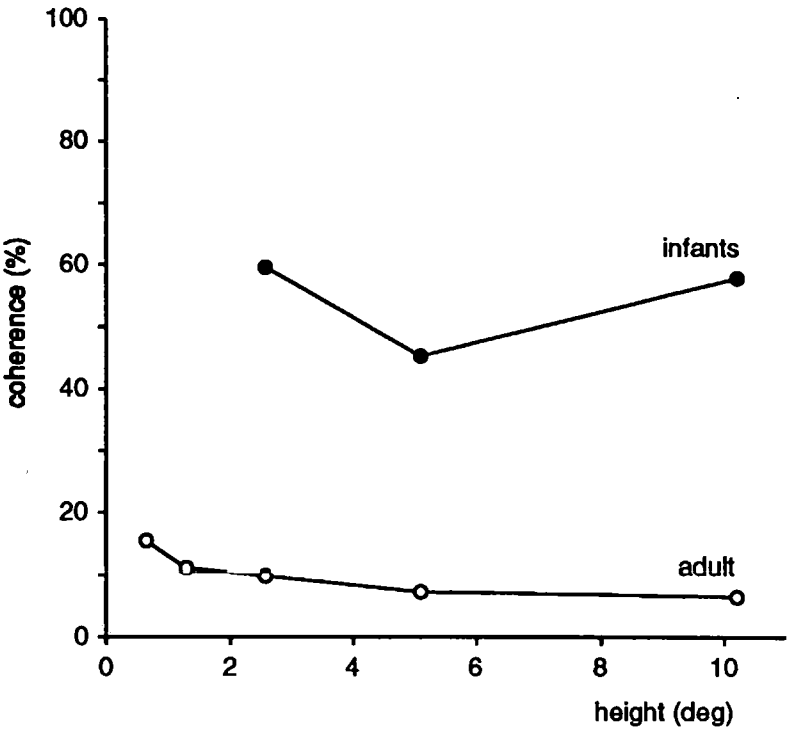

Fig 6.2 Coherence thresholds as a function of the height of the regions of opposite directions in the segregated stimulus (target side). Motion on the non-target side was uniform - all the coherent dots moved in the same direction. Individual data are given in Table 13, Appendix 4.

not suitable for measuring spatial integration.

The second attempt to examine spatial integration used a modified stimulus. On both sides, half of the coherently moving dots moved to the left, while the other half moved to the right. As before, these opposite directions were spatially segregated on the target side (which was therefore the same as in the previous experiment). However on the non-target side the oppositely-moving dots were randomly scattered over the whole rectangle, producing transparent motion. At the point where perceptual segregation of the target breaks down, so that it too appears as transparent motion, the two sides become indistinguishable.

The 10 deg (3 regions) condition was dropped in this experiment, since the odd number of regions does not allow a 50:50 split of the coherent dots between the two directions. Instead the infants were tested with heights of 5 deg (6 regions), 2.5 deg (12 regions) and 1.25 deg (24 regions). As before the reversal interval was 0.48 sec. The results (plotted in Fig 6.3) came from 11 infants; 10 gave results for the 1.25 deg condition, all 11 for 2.5 deg and 9 for 5 deg (Table 14, Appendix 4). In the 1.25 deg

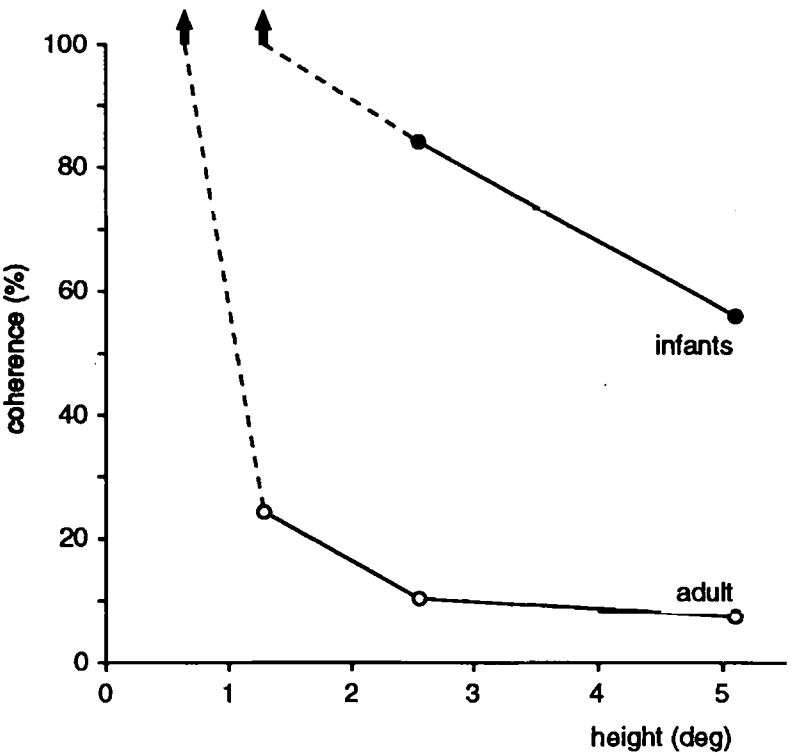

Fig 6.3 Coherence thresholds as a function of region height. This time the non-target side contained transparent motion - the coherent dots were divided equally between left and right motion, but were not spatially segregated. The points plotted as arrows denote median thresholds above 100% - ie the majority of staircases terminated with chance performance at 100% coherence (for the adult's data point plotted as an arrow, all three staircases terminated this way). Note the change of abscissa scale compared with the previous figure. Individual results are shown in Table 14, Appendix 4.

condition only one infant performed above chance at 100% coherence; six had thresholds below 100% at 2.5 deg, and all ten at 5 deg. The difference between the results of these last two conditions was significant (Wilcoxon signed-rank test, $P < 0.01$).

It is evident from Fig 6.3 that the minimum region height that supports segregation is larger for the infants than for the adult. This is analogous to the results for temporal integration (Fig 6.1). However unlike the temporal case, with increasing height the adult's performance reached asymptotic levels before the infants'; infants appear to integrate over larger regions of the stimulus.

Discussion

All three of these experiments indicate a substantial improvement in motion sensitivity

between infants and adults. The same trend is apparent in the infant data alone (Fig 6.4); for the 24 infants tested with the condition shared by the first two experiments, there was a significant negative correlation between coherence threshold and age (r = 0.486; t = 2.625, $P < 0.02$). Forwards extrapolation of the regression equation suggests

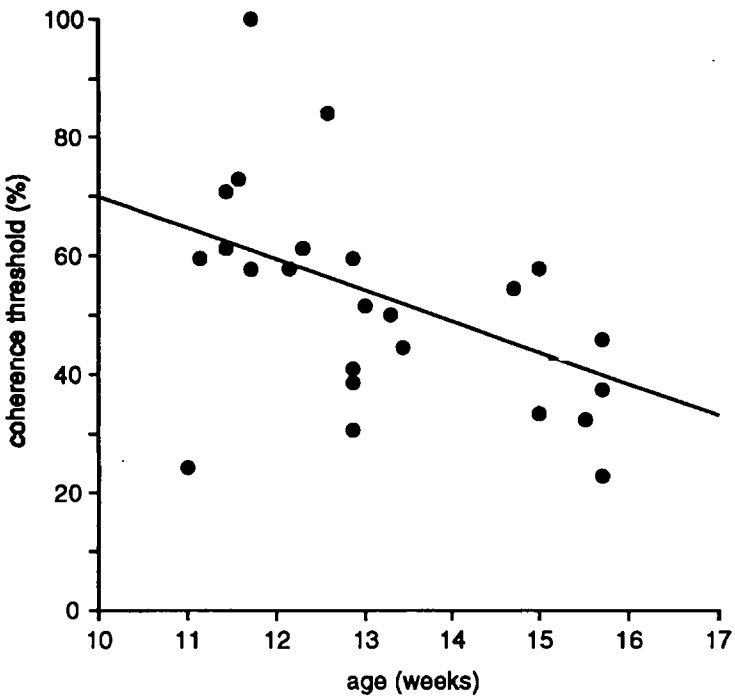

Fig 6.4 Individual coherence thresholds plotted against age for all infants tested with the common condition of the first two experiments (region height 10 deg, reversal interval 0.48 sec).

that adult sensitivity (a threshold of about 5%) would be reached by around 20 weeks, while extrapolating backwards suggests an onset age (a threshold of 100%) of about 5 weeks. Although this agrees quite well with the results of the previous chapter, it should not be taken too seriously; there is no reason to suppose that the linear relationship illustrated in Fig 6.4 is the correct one*, and anyway extrapolation is a poor substitute for experimentation.

It is clear from the results that the improvement in motion sensitivity during development is not due to an increase in the spatial and temporal range of integration. In fact the converse seems to be the case; improvements in sensitivity, by some other means, allow the extraction of directional information from smaller areas and shorter

*Virtually all possible combinations of linear, log, and quadratic regressions were tried; all produced similar correlation coefficients, which implies that the data are too noisy to determine the true relationship. Extrapolated onset ages varied between 4.7 and 7.9 weeks.

intervals. In principle these kind of changes could account for some of the development of d_{max}; the target area and reversal interval used in Chapter 4 might have constrained the performance of younger infants. In practice however, provided that coherence thresholds and d_{max} have similar integration limits, the present results imply that the reversal interval and target width used in Chapter 4 (0.24 sec and 10 deg) were sufficiently large that they would not have been limiting factors, at least for older infants (3 months and above).

In Chapter 4, two alternatives for the development of d_{max} were suggested: a uniform increase in sensitivity at all displacements, and/or a specific improvement for large displacements. The developmental increase in sensitivity found here for an intermediate displacement size clearly implies that the former plays a part. The question remains, is it sufficient to account for the development of d_{max}? The data shown in Fig 6.5 suggests that it may not be. This plots sensitivity [100/(% coherence threshold)] as a function of displacement size for the adult subject, along with the mean sensitivity of

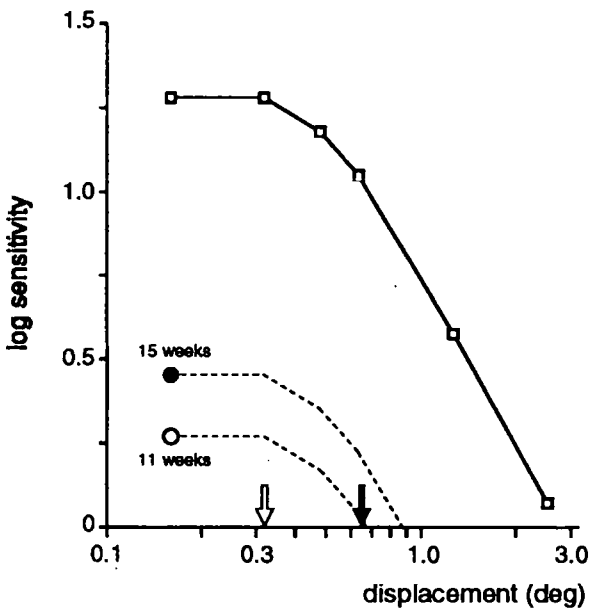

Fig 6.5 Plot of log sensitivty [= 100/(% coherence threshold)] against displacement size for an adult subject (open squares) for discrimination of the segregated from the uniform (single direction) stimulus, with a region height of 10 deg (3 regions) and reversal interval of 0.48 sec. The circles show log mean sensitivity of 11-week (open circles) and 15-week (filled circles) infants from the condition common to the first two experiments of this chapter; ie displacement size 0.16 deg, and other stimulus parameters the same as for the adult data plotted here. The dotted curves are vertically (but not horizontally) displaced copies of the adult sensitivity curve. The arrows show mean d_{max} at 11 weeks (open) and 15 weeks (filled) from the first experiment of chapter 4.

11- and 15-week-old infants at the single displacement size (0.16 deg) used in the experiments above. The broken curves are copies of the adult sensitivity function, shifted down to meet the infant sensitivity values, which show the effect of a uniform reduction in sensitivity. For both 11- and 15-week-olds these curves meet the displacement axis well above the mean values of d_{max} obtained from infants of the same age in Chapter 4. This difference is particularly marked for the younger infants. There is clearly a hint here of a specific increase in sensitivity at large displacements, though the data is too sparse and the comparison between experiments too uncertain to allow a definite conclusion. Fuller measurements of motion sensitivity functions at different ages are needed to clarify this issue.

Finally it is of interest to consider whether these experiments reveal anything about infants' perceptual segregation of the motion stimuli. It is clear that the infant visual system integrates over finite areas to extract direction, and that the results of this are kept sufficiently distinct to allow discrimination between the segregated and unsegregated stimuli. These are the rudiments of segregation. However integration areas are evidently smaller than the largest regions, and it is not clear whether there is any further grouping process that allows the infants to perceive the coherence of each region. Likewise it is by no means certain that information about the spatial layout of the segregated regions is preserved, or that infants perceive sharp borders between them. None of these is logically necessary for performing the task. Experiments on discrimination of motion-defined shapes are probably the best way of addressing this issue; the study of Kaufmann-Hayoz et al (1986) indicates that, at least for the specific case of coherent motion against a stationary background, 3-month-olds are quite capable of such discriminations. It would be interesting to know whether this remains true when the direction of motion is the only cue for segregating the shape from its background.

Conclusions

In these experiments coherence thresholds were used as a measure of motion sensitivity at an intermediate displacement size (0.16 deg). For both adults and infants sensitivity improved as stimulus area and duration increased. The main difference was that infants required larger minimum areas and longer minimum durations in order to

extract motion direction.

Even under the best conditions infants were markedly less sensitive, with mean coherence thresholds of around 50%, compared with 5-7% for the adult. In addition, within the group of infants coherence thresholds were negatively correlated with age. In other words at a displacement size of 0.16 deg there is a progressive improvement in motion sensitivity during development. It is most likely that similar improvements would be found at other displacement sizes, which suggests that at least some of the development of d_{max} found in Chapter 4 results from a uniform increase in sensitivity at all displacements, though it remains possible that further specific improvements in sensitivity to large displacements are also involved.

7 Discussion

In this thesis, the development of visual motion processing in infants has been explored in experiments on the detection of apparent motion in random-dot patterns. Most of the experiments used discrimination of opposite directions as an index of motion detection; direction is a fundamental parameter of motion, and direction discrimination is a robust and specific criterion which is commonly used in adult psychophysics and neurophysiology. Two major themes were addressed in this work. The experiments of Chapters 3 and 4 used the maximum displacement limit for apparent motion (d_{max}) as a measure of motion sensitivity. These experiments charted the development of d_{max}, and also sought to elucidate some of the factors underlying it. The second theme, which was the subject of Chapter 5, concerned the onset of directionality: is sensitivity to direction of motion present at birth, or does it emerge during the first weeks of life? Finally, the experiments on spatiotemporal integration described in Chapter 6 used a different measure of motion sensitivity - coherence thresholds at an intermediate displacement size - to take a first explicit look at more global aspects of motion processing. However integrative processes are fundamental to all aspects of motion perception, and the design of these experiments was aimed as much towards shedding further light on the previous results as on breaking new ground.

The development of d_{max}

The first experiments (Chapter 3) found that d_{max} for the breakdown of coherent motion - ie the discrimination of coherent from incoherent motion - increased with age. However there are theoretical reasons (presented in Chapter 3 and Appendix 3) for supposing that, at least for the stimuli used here, this task does not provide very specific information about motion processing. The experiment on adults in Chapter 4 provided empirical support for this by showing that the coherent vs incoherent task was possible at displacements above those for which direction could be determined.

Exploration of direction discrimination started with the experiments of Chapter 4. The first of these showed that d_{max} for discrimination of opposite directions also increased with age. In many ways this is the central result of the thesis; most of the

remaining experiments were concerned with exploring the reasons for, and implications of this development of d_{max}.

When the interval between coherent displacements was increased from 20 to 40 msec, d_{max} of infants less than 12 weeks old increased, while that of older infants remained unchanged. This suggests that the younger infants are unable to process displacements separated by short intervals, which implies that one factor behind the development of d_{max} is an improvement in the temporal properties of motion detection. Older infants can process displacements at intervals at least as low as 20 msec, which is similar to the lower temporal limit for constant d_{max} in adults (Baker & Braddick, 1985b; Nakayama & Silverman, 1984; Snowden & Braddick, 1989), and implies that the temporal maturation is largely complete by about 12 weeks. However the increase in d_{max} continues well beyond this age. There must be a second more prolonged developmental process which is largely responsible for the increasing d_{max} of older infants, and which may well overlap with the earlier temporal maturation.

The theoretical account of low-level motion processing described in the introduction offers a simple interpretation of these two developmental processes. The first, temporal maturation, represents the emergence of detectors with shorter delays (ΔT), while the second results from the emergence of detectors with larger spans (ΔS). According to this scheme, d_{max} always depends on the largest values of ΔS in the population of motion detectors. However as pointed out in the introduction, motion perception depends not only on the presence of motion detectors, but also on the way in which they are used. Some kind of global combination is necessary to resolve the inherent ambiguity of local motion signals, and this may well lead to a relationship between d_{max} and ΔS which is far from straightforward. Indeed the increase in d_{max} which results from low-pass spatial filtering (Chang & Julesz, 1983b; Cleary & Braddick, 1990b) suggests that the mechanisms with the largest ΔS may not determine d_{max} in spatially broadband patterns. In fact, recent studies suggest that d_{max} represents a limit imposed by the information content of the stimulus, rather than an inherent spatial limit of motion detectors (Eagle, 1992; Morgan, 1992). Specifically, the visual system uses nearest-neighbour matching to establish correspondence between successive frames, and d_{max} occurs when this process starts to produce significant numbers of false matches. Here ΔS does not enter the picture at all, at least as a limiting

factor.

Whatever the relative merits of different theoretical approaches to motion detection, it seems clear that in general terms d_{max} can be viewed as a limit to the visual system's ability to extract signal from noise (eg true matches from false ones). It is also clear that motion detectors are tuned for spatial frequency, and that the deterioration of signal to noise ratio with increasing displacement size will be least rapid in the lowest spatial frequency channels, which should therefore offer the highest values of d_{max}; Eagle (1992) provides evidence that these channels do in fact determine d_{max} in adults. This underlines an important issue concerning the development of d_{max}. The decrease in coherence thresholds with age at an intermediate displacement size found in Chapter 6 implies that there is a uniform improvement in motion sensitivity across all displacement sizes, and this undoubtedly plays a major part in the development of d_{max}. However the rather uncertain comparison between the results of Chapters 4 and 6 (Fig 6.5) suggests there may be additional specific improvements at large displacements. The most likely candidate here would be the emergence of low spatial frequency motion mechanisms (this is of course related to the idea of the emergence of detectors with large spans proposed above). This is an intriguing notion. The usual picture of the infant visual system is one in which at first only coarse spatial scales (ie low spatial frequencies) are represented, with the introduction of processing at progressively finer scales during development. However it is possible that, at least for motion processing, processing is initially at intermediate spatial scales, spreading to both fine and coarse scales during development. Of course this may well also be the case in other visual domains. It clearly deserves further investigation.

These alternatives apply to the second of the two processes identified above as underlying the development of d_{max} - the extended process which dominates development after about 3 months. The first process, which appears to be largely complete by this age, requires an explanation in terms of the temporal properties of motion detection. The general improvement in sensitivity to high temporal frequencies which, at least at low spatial frequencies, follows a similar time course (Regal, 1981; Moskowitz & Sokol, 1980; Hartmann & Banks, 1992) is an obvious candidate (again, this is related to the more specific notion of the emergence of short ΔT detectors suggested above). The fundamental temporal frequency of any given spatial frequency

component in the stimulus depends inversely on the sampling interval (ie the interval between displacements), and directly on the displacement size*. If d_{max} is determined by the signal-to-noise ratio in the lowest available spatial frequency channel, then it will be invariant with changes in sampling interval provided this is sufficiently long to ensure that the temporal frequencies of the relevant spatial frequency components are below the channel's upper temporal frequency cut-off. At shorter intervals there will be a trade-off between temporal frequency and displacement size, so that d_{max} will vary along a line of constant velocity. The displacement interval experiment (Fig 4.3) indicates that for infants aged 12 weeks and above the v_{max} to d_{max} transition occurs at intervals of 20 msec or less. The adult transition interval is similar (Baker & Braddick, 1985b; Nakayama & Silverman, 1984; Snowden & Braddick, 1989) In other words the upper temporal cut-off of the channel determining d_{max} is similar in adults and older infants. In younger infants however the transition occurs at longer intervals (40 msec or above - Fig 4.3), implying a lower high temporal frequency cut-off.

The onset of directionality

The first experiment of Chapter 5 showed that the increase in directional d_{max} with development is linked with a decrease in d_{min}. This confirmed the idea, already implicit in the former result, that the range of displacements (and hence velocities) supporting direction discrimination expands as the infant matures[9]. This in turn raised the question of whether younger infants are sensitive to direction at any displacement, and the rest of the experiments of Chapter 5 explored this. Neither FPL nor habituation experiments gave any evidence for direction discrimination before 6 weeks, though an older group

---

*The apparent motion of these stimuli has a velocity

$$v = d/t,$$

where d is the displacement size, and t is the sampling interval. This is true for the whole pattern, and for any non-aliased spatial frequency component. For a drifting grating of spatial frequency sf

$$v = tf/sf,$$

where tf is the temporal frequency. With sampled motion this is the fundamental temporal frequency; the sampling introduces harmonics of tf. Eliminating v and rearranging gives

$$tf = sf.d/t,$$

as required.

---

[9]Given the substantial rise in d_{max} with age, a non-expanding range would require an equally substantial increase in d_{min}. This is *a priori* most unlikely.

(6-8 weeks) showed clear evidence for it in the habituation experiments. In contrast, infants of all ages appeared able to discriminate coherent motion from a static background, and from incoherent motion. Neither of these tasks requires directionality, though they do provide bounds for the displacement range for directional responses. The success of the younger infants with these control conditions implies a specific impairment of direction discrimination prior to 6 weeks.

On the whole the results suggest that directionality emerges at around 7 weeks of age. If true, this means that its development lags behind that of orientation-selectivity, for which evidence had been found in newborns (Atkinson et al, 1988; Slater et al, 1988). In very young infants, orientation-specific responses are most readily obtained at low temporal frequencies and moderately high spatial frequencies (Braddick et al, 1989b; Hood et al, 1992). This pattern is reminiscent of the characteristic properties of parvocellular neurones (Derrington & Lennie, 1984), which suggests that orientation selectivity first emerges in this pathway. In conjunction with the more delayed development of functions characteristic of the magnocellular system (directionality, binocular disparity, and sensitivity to high temporal frequencies), this has prompted the suggestion that the parvocellular pathway becomes functional before the magnocellular pathway (Atkinson & Braddick, 1990; Braddick, 1993a).

Neurophysiological data on the development of directional selectivity in other species might be expected to shed light on the present results. Unfortunately the available data is sparse, and comes mainly from the cat. Both orientation- and direction-selective neurones are found in the visual cortex of newborn kittens, though initially their selectivity is rather weak and numbers are low, with rapid maturation starting soon after eye-opening (Albus & Wolf, 1984; Price et al, 1988). Interestingly, Albus & Wolf (1984) found few cells that responded to velocities above about 20 deg/sec in newborn kittens, while an increasing proportion did so in older animals, which at least qualitatively mirrors the development of d_{max} found here. There is little direct evidence from these studies that orientation selectivity develops before directional selectivity. However indirect evidence suggesting that it might comes from the study of Swindale et al (1987) on the mapping of orientation and direction selectivity across the cortical surface of area 18 in adult cats. They found that preferred orientation varies smoothly almost everywhere, except for point singularities which were surrounded by 180 deg

cycles of orientation. It is likely that this arrangement develops to meet a requirement for a complete and (as far as possible) smooth representation of both preferred orientation and spatial position on the 2-dimensional cortical surface (Swindale, 1982; Durbin & Mitchison, 1990; Obermayer et al, 1990). If a smooth orientation map is desirable, presumably the same is true for the map of preferred directions. However whereas orientation can only vary over 180 deg, preferred direction varies over 360 deg (the directional neurones in this area are generally oriented, with their preferred direction orthogonal to their preferred orientation). This means that, given the orientation map described above, the smoothest direction map contains lines where preferred direction changes discontinuously by 180 deg, which start and end at point singularities in the orientation map. This was the arrangement found by Swindale et al (1987). It suggests that the development of the direction map is constrained by the orientation map, rather than *vice versa*, which is at least compatible with the idea that directionality develops after orientation selectivity.

As with other forms of cortical selectivity, there is a sensitive period for the development of directionality, in which adequate visual experience is necessary for normal maturation of responses (Daw & Wyatt, 1976). These authors found that, in the kitten, the sensitive period for directional selectivity was much shorter than that for binocularity (ie the establishment of ocular dominance), which matches the present finding that functional directionality emerges before binocularity in human infants. No doubt the rather weakly selective neurones found in newborns act as a seed for this experience-driven development, but it is by no means certain that prior to this development, these neurones are functional in the sense of being able to support perceptual discriminations. Directional neurones may well also be present at birth in human visual cortex, but this is not necessarily incompatible with a later onset of functional directionality. It is of course the latter which is measured in behavioural experiments on motion perception.

Gibson (1966) was among the first to emphasise the central importance of motion in visual perception. It is the spatiotemporal correlation structure of the visual input that provides the most reliable information about the layout of the environment and the observer's movement within it. This view places motion processing at the heart of visual perception. It also emphasises the significance of non-uniform patterns of

motion; both smooth variations and abrupt discontinuities of velocity are fundamental visual cues, whose evolutionary importance has been emphasised by Horridge (1984). Hence it may be sensible to expect that the earliest signs of motion perception will come from responses to non-uniform motion, and this is perhaps the basic reason why, in the experiments of Chapter 5, 6-8-week-olds could discriminate opposite directions in the segregated stimulus, but were apparently not sensitive to the absolute direction of uniform motion. Interestingly one of the earliest behavioural responses to motion is the blink reflex elicited by a looming (and thus non-uniform) visual input. An increase in blink rate caused by looming can be found, though rather intermittently, in 1-month-olds (Yonas & Granrud, 1985). At first the responses do not distinguish between patterns of expansion which indicate impending collision and those that do not; this specificity emerges at a later age. Early development of the blink reflex is obviously a good idea, and it may be a specialised response that develops independently of general-purpose motion processing*; on the other hand it may be an instance of the general principle that ecologically significant patterns of motion will give the earliest evidence of motion sensitivity.

Uniform motion does have an important role in the control of smooth eye movements. Indeed the apparent insensitivity to the absolute direction of uniform motion shown by both age groups in Chapter 5 could be seen as a result of asking the wrong question; while the infants failed to produce responses indicating a perceptual discrimination, most did successfully produce appropriate smooth eye movements to the stimuli. This was particularly true for the older group, which perhaps reflects the emergence of cortical control of eye movements at this time.

The development of cortical control over smooth eye movements mirrors that of direction discrimination found here. This is particularly true for smooth pursuit, which is first seen at 6-8 weeks (Aslin, 1981), and shows a progression from low to high velocities thereafter (Shea & Aslin, 1990). A similar progression is found in the development of symmetrical monocular OKN (Mohn, 1989), which is generally

*I have read somewhere that the blink reflex has a subcortical component, via the pretectum. If so, it may be similar to OKN; initially a purely subcortical reflex with cortical control coming in at a later stage (this may be responsible for the increasing specificity of the response). Unfortunately I cannot find this reference anywhere.

reported to emerge at around 8-12 weeks; however this apparently later onset may be a consequence of the rather high stimulus velocities which are usually used for testing OKN.

The similarities between perceptual and oculomotor development suggests a common underlying substrate of directional mechanisms. Beyond this, however, the two systems may well develop independently at first, with further links (eg the interaction of retinal motion measures with information about eye movements) being established at a later stage. In adult perception these links play a critical role in resolving the ambiguities of retinal motion, allowing for example the unambiguous identification of absolute direction, with or without eye movements. They are presumably equally important for more sophisticated oculomotor control - eg the pursuit of objects against a textured background; to date the development of pursuit has only been studied with uniform backgrounds, which do not generate conflicting retinal motion signals. Successful pursuit in the presence of such signals must involve more complex processing, and may well mature later.

Appendix 1: Sub-pixel positioning

The video screen can be regarded as displaying a continuous image which has been sampled by the array of screen pixels. Each pixel is a uniformly illuminated approximately rectangular area of the screen. Accurate sampling entails setting pixel brightness to the average luminance of the region of the original image covered by the pixel. When the border between rdp elements coincides with the border between pixels, this average, and hence pixel brightness, is either 0 (black) or 1 (white). If these are the only possible values for pixel brightness, the rdp must always be aligned in this way with the pixel array, so that it can only be displaced by a whole number of pixels. However if pixel brightness can take on intermediate values, then intermediate positions and hence displacements are possible. This is illustrated in Fig A1.1 for successive displacements of a quarter of the size of a pixel. The four distinct positions shown (including the fully aligned case) require a total of five linearly-spaced brightness levels between 0 and 1. This relationship holds generally. In practice a graphics mode with 16 levels per pixel was used, giving a resolution of 1/15th of a pixel. Sub-pixel positioning was used for horizontal motion; with 640 pixels across the screen, each 0.08 deg wide, the minimum displacement was 0.0053 deg, and the minimum velocity was 0.27 deg/sec.

It is apparent from Fig A1.1 that the representation of intermediate positions is not exact. The process of sampling introduces artifacts. Their energy is relatively low, and mainly confined to high spatial frequencies, so that they don't intrude much on the sense of smooth coherent motion. Another possible source of artifacts arises from monitor non-linearities. Sub-pixel positioning requires linearly-spaced brightness levels; however most video monitors exhibit a power-law relationship between input voltage and screen luminance. Measurements indicated that this was approximately a square-law function for the monitors used in the experiments, and the input signals were adjusted accordingly. The end result was coherent motion which to adults appeared quite smooth even at the lowest velocity, though with close scrutiny the modulation of pixel brightness at the light/dark edges of the rdp was visible. Perhaps more importantly, the residual artifacts are identical for leftwards and rightwards

motion, and do not provide any extra cue which might aid direction discrimination.

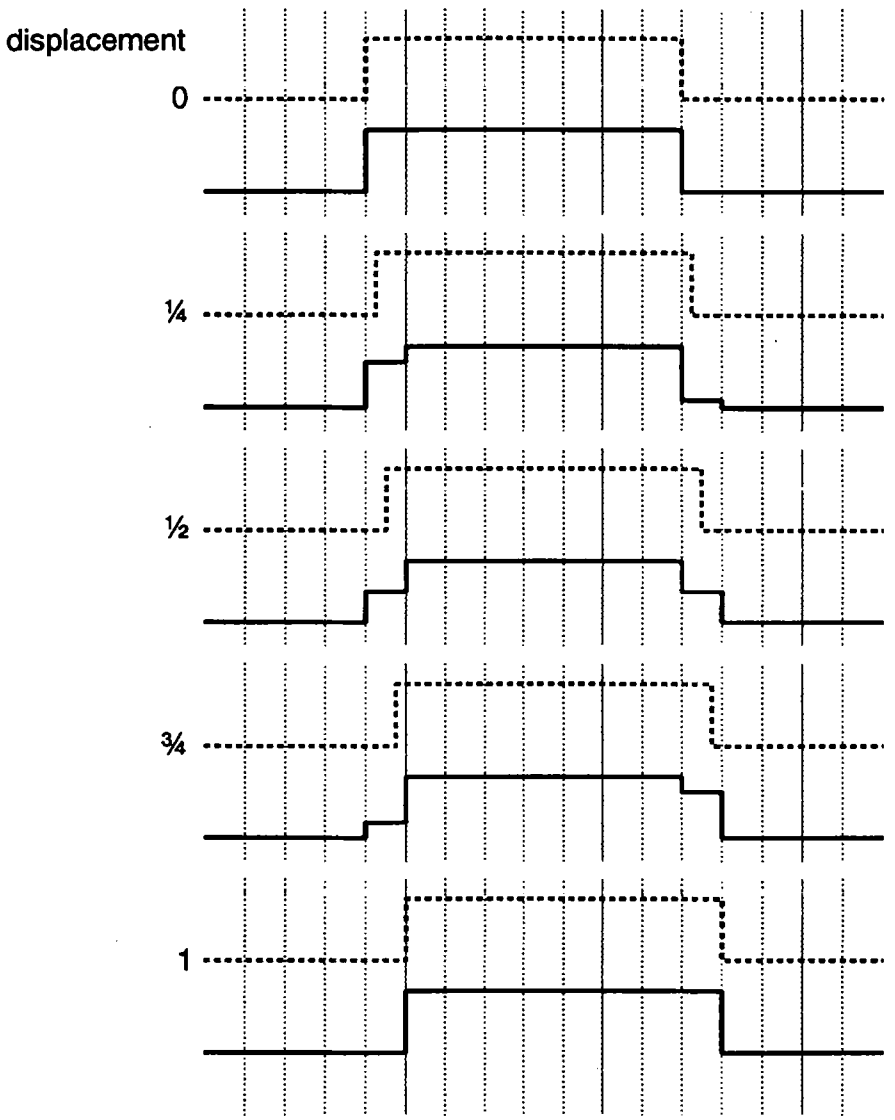

Fig A1.1 Sub-pixel positioning. The vertical lines denote the boundaries between screen pixels, and the broken lines show a white rdp element displaced successively by 1/4 of the pixel width. The pattern of screen luminance resulting from sampling of the rdp by the pixel array is given by the solid lines. The sampling process involves integrating the luminance of the original rdp over the width of each pixel.

Appendix 2: Staircase procedures

Methods of estimating psychophysical thresholds assume an underlying psychometric function with the following general properties: an upper asymptote, where the stimulus is well above threshold and easily detected; a transition region, over which detectabilty declines with increasing stimulus level (this discussion is cast in terms of upper thresholds); and a lower asymptote for levels well below threshold where the stimulus is not detectable. For a two alternative forced choice (2AFC) experiment this translates into a performance of near 100% correct above threshold, declining to 50% correct for stimulus levels well below threshold. The threshold is a measure of the location of the transition region, and is usually given as the stimulus level for a specified detectabilty (performance) somewhere between the upper and lower asymptotes. In the present experiments thresholds were defined as the level giving a performance of 70% correct (for the bracketing staircase), or 70.7% (for the 2-up/1-down staircase).

The most straightforward way of estimating thresholds is the method of constant stimuli. It is also the most inefficient; it require trials at evenly spaced intervals over the whole range of values which covers the possible location of the threshold. Almost inevitably this results in large numbers of trials at levels far from threshold, well into the upper or lower asymptotic regions. If these trials could be eliminated, keeping only those that fall in the transition region, then the threshold could be measured with the same precision but with far fewer trials. This is essentially what staircase procedures attempt to do. They use information from previous trials to choose the stimulus level for the next trial, placing it close to the best current estimate of threshold. Staircases are invaluable for infant psychophysics. With even the best of subjects there is a severe limit to the number of trials that can be gathered before the infant gets bored, and in many cases this make the method of constant stimuli impractical.

The bracketing staircase

This is the procedure that was used to estimate d_{max} in the experiments described in Chapters 3 & 4. It starts with a trial at the smallest displacement level (0.16 deg; this was also the spacing between levels), followed by one trial at each of the next two

higher levels. Stimulus level then steps up between trials until the first incorrect response. Sufficient additional trials are done at this level to decide whether, out of five trials, performance is above or below 70% correct[10]. If it is above 70%, the level is increased, otherwise it is decreased, and performance out of five trials is determined at this new value. This process continues until the current and previous levels between them bracket 70% correct (with 70% or above at the lower displacement, and below 70% at the higher). If necessary trials are added to give the same number at each of these two levels, after which trials alternate between them. If at any time the current pair of levels cease to bracket 70% correct, they are shifted by one step in the appropriate direction. Testing continues until (a) 10-20 trials have been obtained at each of the two levels; (b) these levels continue to bracket 70% correct, and (c) performance is significantly better than chance (binomial $P < 0.05$) at the lower level, but not at the higher level. The level giving 70% correct (the threshold estimate) is then found by linear interpolation. If performance is below 70% at all levels, the trials cycle between the three lowest levels until either performance improves so that the bracketing procedure can be resumed, or 15 have been obtained at each, with performance still below 70%, in which case the staircase is stopped. Fig A2.1 gives an example of a

```
0.16   +                                                    1/1     100.0
0.32    +                                                   1/1     100.0
0.48     +                                                  1/1     100.0
0.64      +    +++ - +                                     5/6      83.3
0.80       -++-   + + +       + + + - + + + +              12/15    80.0
0.96              ++-+--+ - + + - - - - +                  7/15     46.6
```

Fig A2.1 An example of the bracketing staircase. This shows the sequence of trials from the measurement of d_{max} for coherent vs incoherent motion (Chapter 3) in a 9-week-old infant. The column on the left gives the stimulus levels (displacement size in deg), This is followed by the sequence of individual trials, which are shown as '+', for a correct response, or '–', for an incorrect one. Finally the columns on the right show overall performance at each level, first as (number of correct responses)/(number of trials), then as percent correct. d_{max} is defined as the displacement level giving a performance of 70% correct, and is found by linear interpolation between the levels bracketing this performance. In this example these are 0.80 deg (80% correct) and 0.96 deg (46.6% correct), giving a d_{max} of 0.85 deg.

[10]Note that this does not necessarily entail completing 5 trials; for example a performance of 4/4 ensures at least 80% correct with 5 trials.

threshold measurement using this staircase.

The 2-up/1-down staircase

This staircase, which was introduced by Wetherill & Levitt (1965), is one of the most popular choices for 2AFC experiments. Its basic rules are very straightforward: after two consecutive correct responses at a given level the stimulus level is increased, while after a single incorrect response it is decreased. For suprathreshold stimulus values, a response sequence leading to an increase is more likely than one leading to a decrease, while the converse is true below threshold. At the level giving a performance of 70.7% correct, increases and decreases are equally probable. As a result stimulus levels tend to oscillate around this point, with a run of one or more increases being followed by a run of decreases, etc. This produces a sequence of reversals of the direction of changes in stimulus level (ie points at which runs of increases change to decreases and vice versa). The staircase is terminated after a specified number of reversals, and the threshold (defined as the level giving 70.7% correct) is estimated from the mean of the levels at which the reversals occurred. When used with care, this is a fine staircase, and was the first choice for the experiments described here. However it soon became obvious that it has a number of pitfalls, particularly when used with infants, and in the early experiments it was replaced by the more robust but less efficient bracketing staircase described above while these problems were being investigated (see next section).

The final version of the 2-up/1-down staircase used in the present experiments (Chapters 5 & 6) was loosely based on the procedure described by Swanson & Birch (1990). It has additional rules designed to deal with the shortcomings of the basic procedure; motivation for these is given in the next section, which discusses some of the problems encountered when using staircases with infants. The staircase starts at the lowest stimulus level (this description is assumes an upper threshold, though in practice the procedure was used for both upper and lower thresholds). At first, the stimulus level is increased by one step after every correct response. This continues until the first incorrect response; the level at which this occurred is used as the start point for an initial threshold estimate from two reversals of the 2-up/1-down procedure with increments and decrements in steps of two levels at a time. Starting at the level nearest

to this initial estimate, a further six reversals are obtained using a step size of one level. The mean of these six reversals provides the final threshold estimate. If at any time the 2-up/1-down procedure leads to a stimulus level below the point at which the staircase was started, it is replaced by a blocks procedure. This also starts at the lowest level. Trials continue at the same level until either (a) with a minimum of 5 trials performance is above chance (at the 5% level, binomial distribution), in which case the stimulus steps up two levels, and the procedure is repeated, or (b) a total of 20 trials have been obtained and performance is not significantly different from chance, in which case the staircase is stopped and the level one step below the current one provides the final threshold estimate. Whenever possible, the blocks procedure uses results of trials from the failed 2-up/1-down procedure rather than repeating them. Clearly the blocks procedure can terminate with chance performance at the lowest level; if this happens all that can be said is that the threshold is somewhere below this, or more generally that the subject cannot detect the stimulus at any of the available levels. An example of this staircase is shown in Fig A2.2.

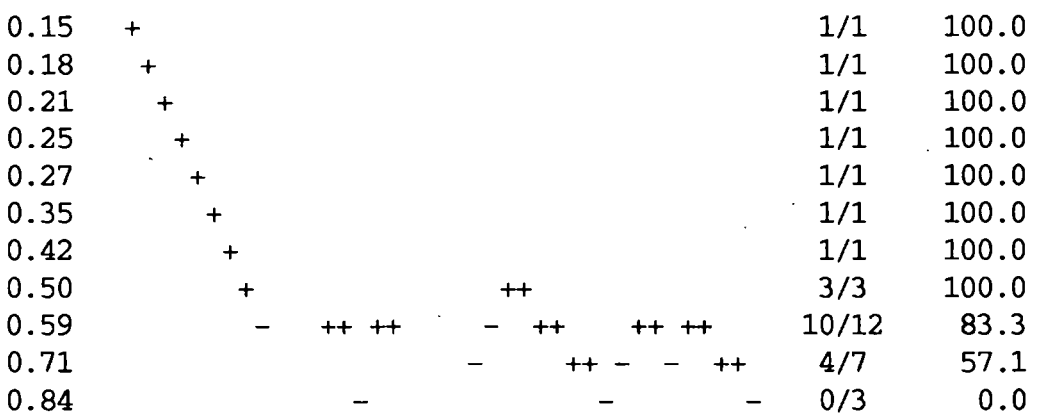

Fig A2.2 An example of the 2-up/1-down staircase. This figure uses the same conventions as Fig A2.1. The staircase is estimating d_{max} of a 13-week-old infant from the first experiment of Chapter 5. d_{max} is given by the mean of the stimulus levels at which the last 6 reversals occurred; in this case it is 0.678 deg.

Problems with the use of staircases with infants

The most serious problem with the basic 2-up/1-down procedure is that it readily terminates with an apparently valid threshold estimate even when the subject's true performance is 50% at all stimulus levels tested. Consider a staircase started well

below threshold. At these levels, where the true performance is 50% correct, reversals are quite likely in either direction (after a step up, the probability of a reversal is 0.75, while after a step down it is 0.25). Thus the overall trend towards lower stimulus levels which is ensured by the staircase rules will have a sequence of reversals superimposed on it, and it is quite possible for the stopping criterion (the specified number of reversals) to be reached before the stimulus levels have fallen below the region of 50% correct performance. The result is a highly inaccurate threshold estimate which depends strongly on the start level but very little on the subject's true threshold. The obvious solution is always to start the staircase at a level that is suprathreshold. However this is not always possible; the subject's threshold may lie below the smallest available stimulus level (as appears to be the case for some subjects in the experiments of Chapter 3), or may not exist at all - ie the subject may be unable to detect the stimulus at any level. This is the reason why the full staircase described above starts at the lowest stimulus level, and transfers to the blocks procedure if the 2-up/1-down rules try to drive the stimulus below the start level; a valid threshold from the blocks procedure depends on a performance that is significantly better than chance at at least one level, which means that the incidence of spurious thresholds from chance performance will be not much greater than the statistical criterion used. The same is true of the bracketing staircase; like the blocks procedure it gives a clear indication of a failure to find a threshold.

Provided that the upper aysmptote of the psychometric function represents a performance of 100% correct, then a staircase started at any above-threshold level will reliably reach the transition region. Unfortunately infants rarely perform this well (and even adults make the occasional mistake). When the upper asymptote is appreciably less than 100% threshold estimates can be strongly biased towards the start point. As before, this is particularly true for the basic 2-up/1-down procedure; if it is started far below threshold, the required number of reversals can be reached while still in the asymptotic region of the psychometric function. Hence it is important that staircases do not start too far from threshold, and this is also desirable in order to avoid using too many of the limited number of trials available from infants in simply reaching the appropriate region of the psychometric function. One solution which has been used is to vary the start level according to the expected threshold of the subject. For example

staircases estimating some threshold which is expected to increase with age would be started at higher levels for older infants. However there is a catch with this; the bias of a staircase towards its start point will tend to produce the expected increase with age even if it doesn't really exist. Clearly in developmental studies a single start point must be used for all staircases. The only way to avoid starting too far from threshold for all subjects is to limit the number of distinct stimulus levels used to span the expected range of thresholds. However increasing the distance between levels by reducing their number will reduce sensitivity to real differences in threshold. Two approaches can be used to reduce the bias resulting from an asymptotic performance of less than 100%, without excessive reductions in the number of stimulus levels: the first is to start the staircase by stepping up one level for each correct response, as in both of the staircases described above. The second is to use a two-stage staircase; an initial rough estimate made with a few widely spaced levels is used as the start point for a staircase with more closely spaced levels. This was incorporated into the full 2-up/1-down procedure.

The final version of the 2-up/1-down staircase was chosen on the basis of computer simulations. The procedure is not necessarily optimal, though the simulations were extensive enough to suggest that increasing the number of trials is the only way to produce substantial improvements. The design of the bracketing staircase, on the other hand, was guided more by intuition than by rigorous analysis. Nevertheless computer simulation indicated that it performs at least as well as the final 2-up/1-down staircase.

The simulations explored the effect of changes to the slope and upper asymptote of the psychometric function on staircase performance. Performance measures were bias and variability (ie mean and standard deviation of the difference between estimated and true thresholds), and mean number of trials, from 100 simulated staircases. Fig A2.3 shows two examples of the psychometric functions used; one with a shallow slope and an asymptote of 90% correct, the other with a steep slope and an asymptote of 100%. Simulation results obtained with these psychometric functions, for both the bracketing and full 2-up/1-down staricases, are shown in Fig A2.4, which plots bias and variability as a function of true threshold between 0 and 18 levels from the staircase start level.

With the good psychometric function (steep slope and 100% asymptote), both staircases perform well. The main difference is that the 2-up/1-down staircase shows a

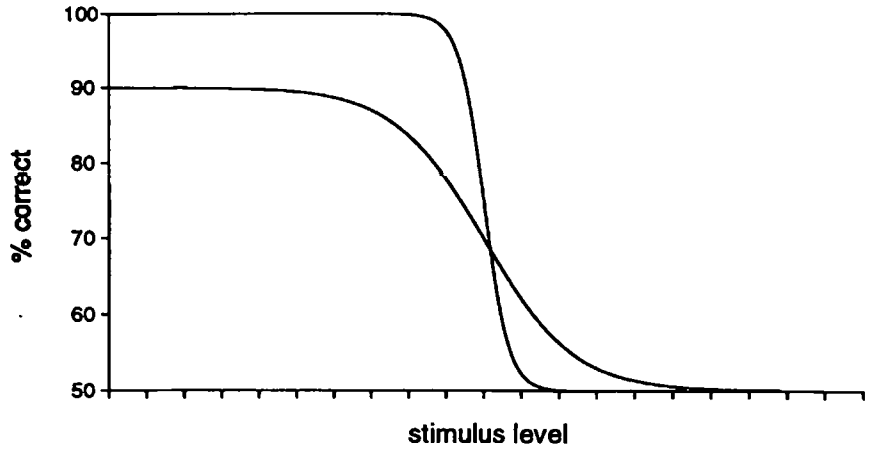

Fig A2.3 Examples of the psychometric functions used in the simulations. They are based on the logistic function; this was an entirely arbitrary choice, since the exact mathematical function used is likely to be far less important than the effect of changes in the two parameters illustrated; the slope (and thus the width) of the transition region, and the performance level of the upper asymptote.

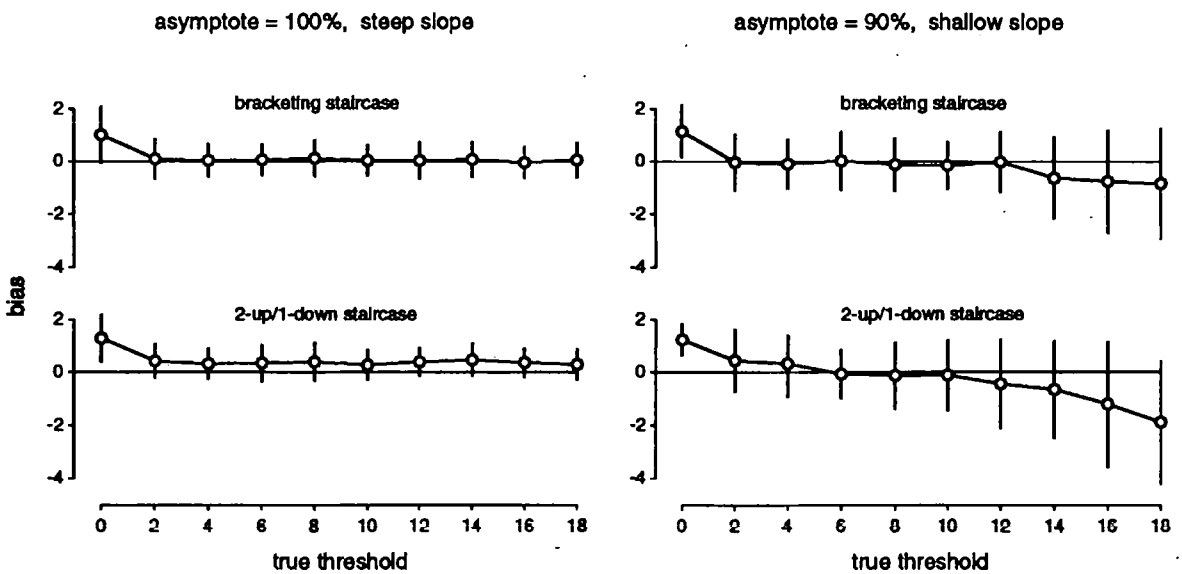

Fig A2.4 Simulation results with the two psychometric functions illustrated in Fig A2.3. Bias and variability (ie mean (circles) and standard deviation (error bars) of the difference between estimated and true thresholds) are plotted as a function of true threshold. The units are stimulus levels; all staircases were started at level 0. A positive bias indicates a threshold estimate which is greater than the true value. The appreciable bias when true threshold is zero occurs because in this case 40-50% of all staircases fail - ie they terminate with an undefined threshold of <0. The plotted data represent only those staircases which gave definite thresholds, and these can never be less than zero.

small positive bias which is independent of the true threshold. The psychometric function with a shallow slope and 90% asymptote produces greater variability and appreciable negative bias at high thresholds. From the full set of simulations, of which only a sample is shown here, it was clear that performance depends mainly on the upper asymptote; by itself a shallower slope leads to slightly greater variability, but little or no bias. The simulations also included the case of a flat psychometric function - chance performance at all levels. The incidence of spurious thresholds was 13.7% for the bracketing staircase, and 12.8% for the 2-up/1down staircase

On the whole the simulations suggested that the bracketing staircase performs slightly better than the 2-up/1-down staircase. However the latter does have a significant advantage; in the simulations it required 30-40% fewer trials to reach threshold. This was also true in the experiments; over all infants tested, the mean number of trials for the 2-up/1-down staircase was 37.8 (standard deviation 8.2), compared with 46.6 (12.8) for the bracketing staircase. Nevertheless the overall conclusion from the simulations was that with infants the choice of staircase is not too critical. The most important thing is to ensure that it is well behaved when the upper asymptote of the psychometric function is below 100%, and when the threshold either doesn't exist or is below the lowest available stimulus level.

One issue which has not been discussed so far concerns the spacing of stimulus levels. An even spacing over the desired range is obviously sensible, but should this be along a linear or logarithmic scale? In principle the appropriate scale is one in which the shape of the psychometric function does not depend on its location (ie threshold), but in practice the information needed to identify this was not available. On the whole a logarithmic spacing seems the most sensible way of spanning a wide range of possible thresholds; it ensures that errors arising from the gap between stimulus levels are a constant percentage of threshold over the whole range. However logarithmic spacing is not always practical. For example in the first experiment of chapter 4, the smallest possible increment in displacement was 0.16 deg; with strict logarithmic spacing the range between the lowest available displacement (also 0.16 deg) and adult thresholds (around 2 deg) would be covered by less than five levels, and the infants' threshold range by just over three. This is clearly too few levels, and in the experiments subject to the 0.16 deg limit (all those described in Chapters 3 and 4), linear spacing was used.

The other experiments were not limited in this way, and the stimulus values could be logarithmically spaced.

Appendix 3: The response of low-pass mechanisms to coherent and incoherent motion

This appendix describes in more detail the responses of low-pass spatiotemporal mechanisms to coherent and incoherent motion in rdps. For simplicity, only one spatial dimension will be considered, and coherent displacements will always be an integer multiple of the rdp element size. Motion occurs in discrete steps; a static rdp is displayed for m msec (the monitor's frame interval) before being instantaneously replaced by either a shifted version of itself (coherent displacement) or a new, uncorrelated pattern (incoherent jump), which in turn is displayed for a further m msec etc.

Consider first the response, $r(t)$, of a purely spatial mechanism (ie one that passes all temporal frequencies) as a function of time. The structure of $r(t)$ can be described by its autocorrelation function,

$$a(u) = \int_{-\infty}^{\infty} r(t)\, r(t+u)\, dt$$

which is a measure of the extent to which the response at time t is correlated with the response at time $t+u$. Evidently this will be at a maximum when $u=0$; $r(t)$ is always 100% correlated with itself. When the input consists of incoherent motion, then by definition responses separated by intervals of m msec or more are completely uncorrelated, ie

$$a(u) = 0, \quad u \geq m,$$

and it is fairly straightforward to see that $a(u)$ decreases linearly between $u=0$ and $u=m$ [Fig A3.1(a)]. With incoherent motion, this pattern is found whatever the spatial receptive field profile of the mechanism. However with coherent motion, $a(u)$ does depend on the mechanism's spatial properties. For a receptive field consisting of a single point, coherent and incoherent motion produce identical autocorrelation functions; the mechanism can only see a single element at one time, so that the spatially uncorrelated structure of the random-dot pattern translates into a temporally uncorrelated structure in the mechanism's response for intervals $\geq m$. With larger receptive fields however, coherent (but not incoherent) motion results in correlated

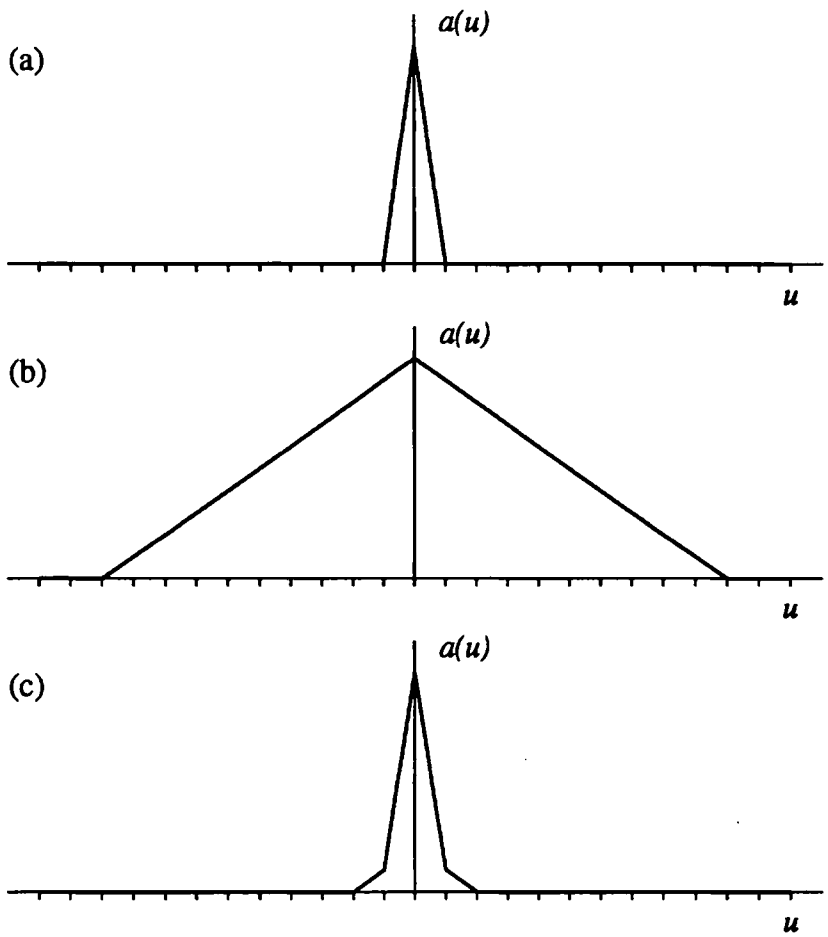

Fig A3.1 Temporal autocorrelation functions of the responses of spatial mechanisms to motion sequences. The scale of the abscissa is in units of m msec (the monitor's frame interval). (a) Incoherent motion; the autocorrelation function is independent of the spatial receptive field profile. The same pattern is obtained with coherent motion whenever the displacement size is greater than the width of the receptive field. (b) Coherent motion, for a displacement size of 1 element and a receptive field with a rectangular profile 10 elements wide. (c) Coherent motion, displacement size 9 elements; same receptive field as (b).

responses over longer intervals. For example, consider a mechanism which simply integrates luminance over 10 adjacent rdp elements (thus acting as a low-pass spatial filter). After a single coherent displacement of one rdp element, 9 out of the 10 elements that it sees are the same ones that it saw before the displacement, and the two responses will show 90% correlation (note that the mechanism is not sensitive to the spatial layout of the elements forming its input). Similarly, responses separated by two displacement intervals will be 80% correlated, and so on, and it is not until intervals of ten displacements or more that the responses become uncorrelated. Hence the

autocorrelation function, $a(u)$, has a width of $20m$ msec[11] [Fig A3.1(b)], ten times wider than $a(u)$ for incoherent motion. Increasing displacement size will reduce the width of $a(u)$; for example, its width is $10m$ with displacements of 2 elements. After a single displacement of 9 elements correlation is only 10% and falls to zero after a second displacement of this size, giving an $a(u)$ which is very close to that for incoherent motion [Fig A3.1(c)], while for displacement sizes of 10 or more elements, $a(u)$ is identical to that produced by incoherent motion. Clearly the autocorrelation function of this mechanism's response could in principle be used to discriminate between coherent and incoherent motion upto a limit (d_{max}) of 9 rdp elements. It is also clear that a mechanism with a larger receptive field (a more severe low pass spatial filter) will have a higher d_{max}.

So far, we have a means of discriminating coherent from incoherent motion based on the temporal structure of a spatial mechanism's response $r(t)$, as revealed by its autocorrelation function. However, what we are looking for is discrimination based on differences in response intensity. A suitable measure of intensity is the mean square value of the response, which is equal to the value of $a(u)$ at $u=0$; for purely spatial mechanisms of the kind considered so far, $a(0)$ is the same for both types of motion (Fig A3.1). The solution to this problem, the conversion of differences in temporal structure into intensity differences, is to introduce a stage of low-pass temporal filtering. This is most easily understood in the temporal frequency domain. The temporal power spectrum of a mechanism's response is given by the Fourier transform of its autocorrelation function (Bracewell, 1986),

$$R(f) = \int_{-\infty}^{\infty} a(u)\, e^{-i2\pi uf}\, du$$

Narrow autocorrelation functions give broad power spectra (plenty of power at high temporal frequencies), and vice versa. Fig A3.2 shows the power spectra of $r(t)$ of the mechanism discussed above for incoherent motion, and for coherent motion with a displacement size of two elements. The coherent motion, with its broad $a(u)$, produces a narrow spectrum with most of the power at low temporal frequencies, while the

[11]The autocorrelation function is calculated for both positive and negative values of u, and is an even function [$a(u) = a(-u)$]; hence the non-zero part of $a(u)$ is 2 times wider than the interval over which the correlation is non-zero.

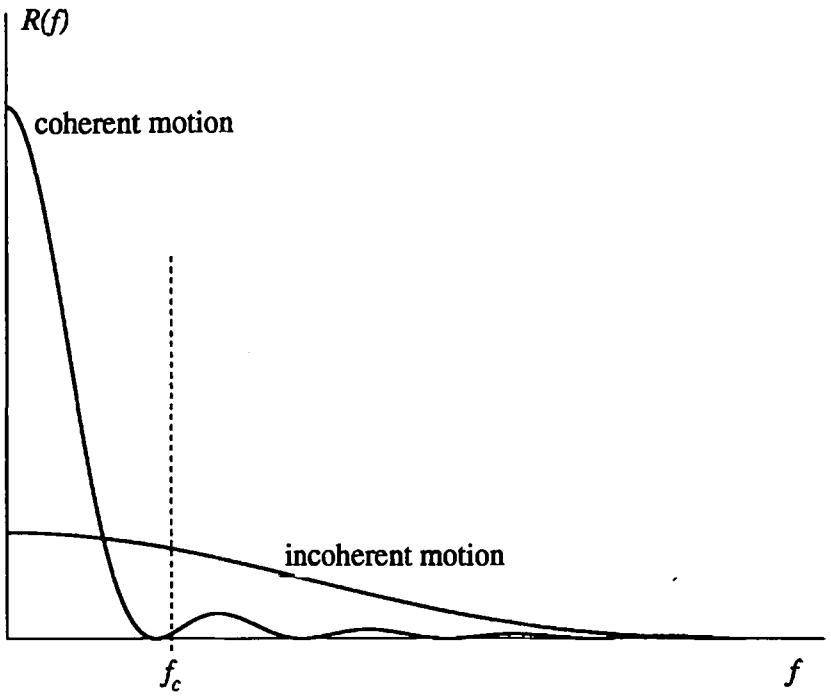

Fig A3.2 Temporal power spectra of the response of the spatial mechanism to incoherent motion, and to coherent motion with a displacement size of 2 elements. The mechanism has a receptive field 10 elements wide. The broken line shows the cut-off frequency of the simple temporal filter discussed in the text, which passes all frequencies less than f_c, and removes all those above it.

spectrum for incoherent motion spreads out to much higher frequencies. Just as for the autocorrelation function, the spectrum for coherent motion becomes progressively more similar to that for incoherent motion as displacement size increases; beyond d_{max} they are identical. Note that the overall power, ie the mean square value of $r(t)$, which equals $a(0)$, which in turn equals the area under $R(f)$, is the same in both cases. Now consider the effect of low-pass temporal filtering. The simplest case is a filter which removes all components above a given cut-off frequency, f_c, as illustrated by the vertical line in Fig A3.2. As before, response intensity after filtering is given by the area under $R(f)$, but now we only need to consider the interval to the left of f_c. In the example of Fig A3.2, it is clear that the temporal filter passes nearly all the power of the coherent motion spectrum but only about half the power of the incoherent motion, giving a response intensity ratio of 2:1 in favour of coherent motion. It is also clear that this ratio will decrease as the coherent spectrum becomes more similar to the incoherent one, ie as displacement increases. In addition, the response ratio at a given

displacement size is increased by more severe temporal filtering (moving f_c to the left).

The analysis so far has been based on expected values of the variables involved; ie those obtained from averaging over infinitely long motion sequences. Under these ideal circumstances, d_{max} depends only on the width of the spatial receptive field. Although a temporal filter is required in order to generate larger responses to coherent motion, its characteristics do not determine d_{max}. In practice of course, responses will be averaged over a finite period, either as a result of limited stimulus duration, or more generally as a result of the visual system using a limited temporal window. Discrimination will be based on an estimate of the expected response intensity, which is a random variable (the stimulus is a *random* dot pattern; internal noise may also play a part), and will only be possible for response ratios significantly greater than 1. This has a number of consequences. First, d_{max} will be appreciably smaller than the width of the receptive field (even for the highly unrealistic rectangular profile used here), though still highly dependent on it. Second, the characteristics of the temporal filter become relevant; reducing f_c will produce a modest (perhaps insignificant) increase d_{max}. Third, for values less than the internal temporal window used by the visual system, d_{max} will depend on stimulus duration. In particular, with very short stimuli (ie a single displacement) simple low-pass mechanisms may be very poor at discriminating between coherent and incoherent motion.

The mechanisms considered so far consist of a spatial filter followed by a temporal filter. However these are linear filters, so their order is irrelevant; an analysis in which the filters were the other way round would give the same result. For simplicity, mechanisms with very unrealistic spatial and temporal properties have been considered. However, although details such as the exact shape of the functions plotted in the figures will vary, the general conclusions apply equally to more realistic mechanisms. Mechanisms that act as low pass spatial and temporal filters respond more strongly to coherent than to incoherent motion; as displacement size increases, the coherent motion response decreases, and will eventually become (statistically) indistinguishable from the response to incoherent motion (d_{max}). d_{max} depends on the spatial and, to a much smaller extent, temporal characteristics of the mechanism, and the best way to increase d_{max} is to employ mechanisms with larger receptive fields.

Discrimination of coherent from incoherent motion by the method described here

does not depend on knowing the direction of the coherent motion. For the two dimensional case, isotropic (ie circular) spatial mechanisms are entirely adequate, and these will respond equally to all directions of motion. In practice, of course, orientation selective mechanisms may be involved, and they will in general give different responses to orthogonal directions. However oriented mechanisms will show identical responses to opposite directions of motion along any axis. The approach described here cannot be used for tasks involving discrimination of opposite directions, such as those used in the experiments of chapter 4. For this discrimination, the additional property of directional selectivity is required.

Appendix 4: Individual data

The following tables give the results obtained from individual infants in the experiments described in this thesis.

Notes

1. Unless otherwise stated, the bottom row(s) give the mean (above) and standard deviation (below) of the individual data in that column.
2. Subjects' ages are given in weeks and days; thus 6w3 means 6 weeks and 3 days.
3. Displacement thresholds are in degrees.

Table 1: d_{max} for discrimination of coherent from incoherent motion.

9-10 weeks		11-12 weeks		13-16 weeks	
age	d_{max}	age	d_{max}	age	d_{max}
9w5	1.34	11w0	0.67	15w0	2.20
10w4	0.73	11w6	1.71	16w5	2.30
9w0	0.67	11w3	0.35	15w2	1.33
9w1	0.85	12w0	1.28	14w3	1.06
10w0	1.56	12w3	1.32	13w6	1.36
9w1	0.37	11w5	1.89	15w0	1.58
9w6	0.43	12w6	1.60	13w3	1.65
10w6	1.01			15w5	1.96
9.79	0.87	11.90	1.26	14.95	1.68
	0.42		0.56		0.44

Table 2a: d_{max} for discrimination of opposite directions

8-9 weeks		10-11 weeks		12-13 weeks		14-15 weeks	
age	d_{max}	age	d_{max}	age	d_{max}	age	d_{max}
8w5	<0.16	10w5	<0.16	12w5	0.16	14w0	0.36
8w4	<0.16	11w3	0.20	12w3	0.34	14w5	0.48
8w2	<0.16	11w0	0.21	13w0	0.37	15w5	0.48
9w4	<0.16	10w1	0.22	12w3	0.37	14w5	0.54
8w1	<0.16	10w0	0.22	13w6	0.41	15w1	0.56
8w3	<0.16	11w4	0.23	13w3	0.53	14w1	0.64
9w1	<0.16	10w5	0.25	13w5	0.55	15w3	0.67
9w2	<0.16	10w5	0.32	12w6	0.56	15w5	0.69
8w3	<0.16	11w2	0.35	12w0	0.64	14w5	0.71
9w1	0.23	10w1	0.39	13w1	0.70	14w1	0.72
8w2	0.24	11w1	0.40			15w3	0.85
9w6	0.24	11w4	0.53				
9w5	0.25	10w6	0.58				
9w1	0.27						
8w4	0.32						
9w4	0.32						
9w1	0.35						
8w5	0.37						
9w2	0.39						
9w1	0.42						
9w0	0.53						
9w3	0.64						
9w0	<0.16						
8w4	0.19						
8.97	0.235¶	10.87	0.25¶	12.96	0.47¶	14.87	0.64¶

¶median d_{max}

Table 2b: FPL performance (% correct out of 15 trials) of the 8-9-week-olds with $d_{max} < 0.16$ deg

age	0.16†	0.32†	0.48†
8w5	46.7	40.0	66.7
8w4	64.3‡	53.3	26.7
8w2	66.7	40.0	60.0
9w4	60.0	66.7	53.3
8w1	53.3	26.7	40.0
8w3	40.0	46.7	33.3
9w1	53.3	46.7	40.0
9w2	66.7	33.3	53.3
8w3	53.3	66.7	33.3
9w0	66.7	60.0	40.0
	57.5	48.0	44.7

†displacement size (deg) ‡14 trials

Table 3: effect of contrast on d_{max}

age	48%	88%
10w5	0.42	0.43
10w5	0.72	0.22
11w2	0.69	0.69
11w0	0.72	0.53
10w4	0.72	0.18
10w2	0.35	0.56
10w0	0.38	0.84
11w3	0.69	0.51
11w1	0.88	0.24
10w6	0.53	1.10
10w6	0.41	0.52
10.81	0.59	0.53
	0.17	0.28

Table 4: effect of displacement interval on d_{max}

8-11 weeks			12-15 weeks		
age	20 msec	40 msec	age	20 msec	40 msec
8w3	0.34	0.38	12w4	0.37	0.40
9w6	<0.16	<0.16	12w5	0.24	0.22
9w1	0.69	0.69	12w5	0.53	1.0
8w4	0.24	0.39	14w1	0.56	0.83
9w0	<0.16	0.72	15w2	1.17	0.83
9w0	<0.16	0.21	12w5	0.72	0.56
8w6	<0.16	0.34	14w3	0.68	0.77
10w4	<0.16	0.24	14w1	0.35	0.43
10w1	0.24	0.69	15w5	1.01	0.88
9w4	<0.16	0.27	13w0	1.07	0.91
9w4	<0.16	<0.16	12w5	0.56	0.36
11w3	0.24	0.7	13w1	1.36	0.19
10w6	0.57	1.07			
9.59		0.36¶	13.59	0.706	0.638
				0.344	0.288

¶median d_{max}

Table 5: Adults' d_{max}

absolute direction	opposite directions	coherent vs incoherent
2.98	1.68	6.46
3.74	1.76	5.04
4.34	2.30	5.80
3.69	1.91	5.77
0.68	0.34	0.71

Table 6: d_{min} & d_{max}

10 weeks age	d_{min}	d_{max}	13 weeks age	d_{min}	d_{max}
10w4	0.148		13w0	0.043	
10w2	0.045		13w0	0.149	0.276
10w0	0.07	0.189	13w3	0.082	0.393
10w2	0.129		13w2	0.032	0.512
10w1	0.077	0.29	13w3	0.027	0.652
10w2	0.151	0.384	13w3	0.101	
10w6	0.196	0.287	13w1	0.023	0.865
10w4	0.132	0.179	13w6	0.041	0.663
10w5	0.073	0.241	13w5	0.051	0.678
10w2	0.13	0.356			
10w0	0.076	0.294			
10w5	0.128				
	0.133	0.278		0.061	0.577
	0.044	0.073		0.042	0.198

Table 7a: 3-6-week-olds preferential looking (1st group): direction discrimination

		% correct at displacement size (deg)				
age	trials	0.027	0.053	0.107	0.213	0.427
5w0	20	60.0	50.0	50.0	45.0	35.0
6w6	15	46.7	**20.0**	46.7	**26.7**	66.7
3w0	16	**75.0**	50.0	62.5	50.0	62.5
5w5	10	70.0	70.0	60.0	50.0	30.0
6w2	19	47.4	36.8	57.9	57.9	31.6
4w3	12	**16.7**	41.7	41.7	66.7	58.3
6w3	13	53.8	53.8	**76.9**	38.5	46.2
5w4 *a*	14	50.0	57.1	42.9	50.0	57.1
4w5 *b*	16	50.0	56.3	68.8	43.8	62.5
6w1 *c*	17	52.9	52.9	52.9	70.6	**76.5**
5w2 *d*	15	66.7	33.3	60.0	**86.7**	53.3
5.7	15.2	53.6	47.4	56.4	53.3	52.7
		15.5	13.6	10.9	16.5	15.2

Individual results significantly above or below chance (one-tailed binomial $P < 0.05$ for each) are shown in bold.
Italic letters identify the same subjects in this and the next two tables.

Table 7b: 3-6-week-olds preferential looking (1st group): coherent vs static

		% correct at displacement size (deg)				
age	trials	0.027	0.053	0.107	0.213	0.427
5w4 *a*	20	40.0	50.0	60.0	**90.0**	**100.0**
4w5 *b*	15	60.0	53.3	66.7	53.3	73.3
3w0 *e*	10	**80.0**	50.0	50.0	**80.0**	**100.0**
6w6 *f*	10	50.0	60.0	60.0	**80.0**	**90.0**
5w2 *d*	15	73.3	60.0	40.0	53.3	**80.0**
5.1	14.0	60.7	54.7	55.3	71.3	88.7
		16.4	5.1	10.4	16.9	11.9

Table 7c: 3-6-week-olds preferential looking (1st group): coherent vs incoherent

		% correct at displacement size (deg)				
age	trials	0.027	0.053	0.107	0.213	0.427
4w5 *b*	11	72.7	**81.8**	**90.0**	**81.8**	63.6
6w1 *c*	18	61.1	**83.3**	**83.3**	**88.9**	**88.9**
5w6	15	**80.0**	53.3	**80.0**	73.3	73.3
3w0 *e*	20	50.0	65.0	**90.0**	**80.0**	70.0
5w1	10	**90.0**	60.0	60.0	50.0	60.0
6w6 *f*	23	**82.6**	**82.6**	**86.9**	**82.6**	**86.9**
5.3	16.2	72.7	71.0	81.7	76.1	73.8
		14.8	13.2	11.3	13.7	11.9

Table 8a: 3-6-week-olds preferential looking (2nd group): direction discrimination

		% correct at displacement size (deg)			
age	trials	0.107	0.213	0.427	0.853
6w3	20	**75.0**	50.0	50.0	60.0
5w6 *a*	15	40.0	53.3	40.0	26.6
6w2 *b*	15	33.3	53.3	40.0	66.7
5w0	15	33.3	40.0	46.7	46.7
3w4 *c*	15	46.7	33.3	53.3	53.3
6w4 *d*	18	50.0	55.6	55.6	33.3
4w0	10	30.0	30.0	50.0	40.0
4w2	20	60.0	45.0	50.0	60.0
5w5 *e*	18	55.6	50.0	55.6	66.7
5w5	20	**20.0**	55.0	45.0	40.0
5.3	16.6	44.4	46.6	48.6	49.3
		16.4	9.2	5.7	14.1

Individual results significantly above or below chance (one-tailed binomial $P < 0.05$ for each) are shown in bold.
Italic letters identify the same subjects in this and the next table.

Table 8b: 3-6-week-olds preferential looking (2nd group): coherent vs incoherent

		% correct at displacement size (deg)				
age	trials	0.107	0.213	0.427	0.853	1.71
5w6 *a*	20	**75.0**	**80.0**	60.0	**75.0**	60.0
6w2 *b*	14	**85.7**	**78.5**	57.1	35.7	57.1
3w4 *c*	12	75.0	75.0	66.7	66.7	50.0
6w4 *d*	15	73.3	73.3	46.7	66.7	46.7
5w5 *e*	14	**85.7**	**78.6**	**100.0**	64.3	64.3
5.6	15.0	78.9	77.1	66.1	61.7	55.6
		6.2	2.8	20.3	15.0	7.2

Table 9: 3-5-week-olds habituation (segregated vs uniform)

	preference for segregated stimulus (%)			
age	opposite directions‡	coherent vs static†	coherent vs incoherent†	coherent vs incoherent‡
3w0	52.0	76.2	66.8	
4w3	0.0	63.6	58.7	
5w4	47.4	82.4	91.5	
4w1	42.6	51.0		
5w6	71.0	53.5		
3w1	56.3	100.0	43.6	
5w4	35.7	57.4	66.4	
4w5	38.2	64.7	13.1	
4w0	50.0	60.0	53.5	
5w6	34.2	75.5	50.5	
5w6	66.1			57.6
3w3	26.0			81.0
5w4	62.0			71.4
4w5	56.5			67.6
5w5	32.0			87.0
4.77	44.7	68.4	55.5	72.9
	18.0	15.1	22.4	11.5

†test trials only ‡full habituation

Table 10: 6-8-week-olds habituation (segregated vs uniform)

	preference for segregated stimulus (%)		
age	opposite directions‡	coherent vs static†	coherent vs incoherent†
7w1	43.3	50.0	54.3
8w1	73.0	51.5	33.3
7w5	85.4		
8w2	64.1	73.8	57.4
6w1	69.5	60.4	45.4
7w1	51.6	70.4	55.9
7w2	58.0	46.9	73.3
7w1	61.8	97.9	72.5
8w2	66.9	92.0	47.0
7.48	63.7	67.9	54.9
	12.2	19.3	13.5

†test trials only ‡full habituation

Table 11a: 3-5-week-olds habituation (left vs right uniform motion)

	preference for novel stimulus (%)	
age	0.24 deg†	0.16, 0.24 & 0.32 deg†
5w1	10.5	
4w1	60.0	58.4
5w0	77.3	52.7
4w6	39.1	65.2
5w2	46.9	70.5
5w0		22.2
3w0	67.2	
4w1	45.1	53.2
5w2		17.5
5w3	23.4	
3w0	23.9	8.6
4w1	70.5	32.1
3w0	28.3	
5w5		53.9
4w2	31.4	50.4
4w6	63.0	63.8
4w3	60.3	59.4
4w1	39.1	80.4
4w1	33.0	74.6
4.47	47.5	48.1
	21.4	19.9

† displacement sizes

Table 11b: 6-8-week-olds habituation (left vs right uniform motion)

	preference for novel stimulus (%)	
age	0.24 deg†	0.16, 0.24 & 0.32 deg†
6w4	51.7	
8w4	25.6	
6w5	36.3	
8w5	37.6	
7w5	45.7	87.3
9w4		46.0
6w6	68.5	16.5
7w4	75.0	50.0
8w6	38.2	82.8
8w4		50.9
6w1		66.5
6w1		19.6
6w2	63.6	38.0
6w5		74.0
6w4	40.8	
6w5	57.4	28.1
8w1	42.5	
8w0	46.0	59.3
7w4	53.4	35.3
8w3	88.3	54.2
8w6		47.7
7.59	51.4	50.4
	16.7	21.2

† displacement sizes

Table 12: Temporal integration

	Coherence thresholds (%) at reversal interval (sec)		
age	0.12	0.24	0.48
15w5		27.3	22.9
14w5	>100.0	48.5	54.5
11w5		68.7	57.7
15w5		61.2	45.9
13w3		44.5	44.5
12w2	>100.0	64.8	61.2
11w4	>100.0	64.8	
12w6	59.5	66.7	59.5
12w6	38.6	26.5	30.6
11w3	63.0	54.5	61.2
11w4	84.1	42.0	
15w0	>100.0	53.0	33.4
15w4	84.1	61.2	32.4
11w3	>100.0	>100.0	70.7
13w0	66.7	68.7	51.5
13.26	84.1¶	61.2¶	51.5¶

¶median coherence threshold

Table 13: Spatial integration (1)

	Coherence thresholds (%) at stripe width (deg)		
age	2.5	5	10
13w2	38.6	54.3	50.0
11w0	35.6	38.6	
12w6	36.4	30.6	40.9
11w1	>100.0	48.6	59.5
15w5	59.5	42.0	37.5
15w0	77.1	36.4	57.8
11w4	48.6	40.9	72.8
12w4	84.1	59.5	84.1
11w5	>100.0	84.1	>100.0
12w6		23.6	38.6
12w1	51.5	57.8	57.8
11w0	>100.0	>100.0	24.3
12.57	59.5¶	45.3¶	57.8¶

¶median coherence threshold

Table 14: Spatial integration (2)

	Coherence thresholds (%) at stripe width (deg)		
age	1.25	2.5	5
11w4	>100.0	>100.0	84.1
12w0	>100.0	>100.0	56.1
16w0	>100.0	>100.0	42.0
11w5	>100.0	68.4	84.1
12w1	>100.0	86.6	51.5
15w6	>100.0	>100.0	56.1
14w3	84.1	84.1	36.4
12w4	>100.0	77.1	59.5
15w1	>100.0	34.4	
12w1		>100.0	36.4
15w2	>100.0	37.5	
13.53	>100.0¶	84.1¶	56.1¶

¶median coherence threshold

References

Adelson, E. H. & Bergen, J. (1985). Spatio-temporal energy models for the perception of motion. *Journal of the Optical Society of America*, **A2**, 284-299.

Albus, K. & Wolf, W. (1984). Early postnatal development of neuronal function in the kitten's visual cortex: a laminar analysis. *Journal of Physiology*, **348**, 153-158.

Anderson, S. J. & Burr, D. C. (1985). Spatial and temporal selectivity of the human motion detection system. *Vision Research*, **25**, 1147-1154.

Anderson, S. J. & Burr, D. C. (1987). Receptive field size of human motion detection units. *Vision Research*, **27**, 621-635.

Arterberry, M. E. & Yonas, A. (1988). Infants' sensitivity to kinetic information for three-dimensional object shape. *Perception and Psychophysics*, **44**, 1-6.

Aslin, R. N. (1981). The development of smooth pursuit in human infants. In Fisher, D. F., Monty, R. A. & Senders, J. W. (Eds), *Eye movements: Cognition and visual perception.* Hillsdale, NJ: Erlbaum.

Aslin, R. N. (1987). Motor aspects of visual development in infancy. In Salapatek, P. & Cohen, L. B. (Eds), *Handbook of infant perception.* London: Academic Press.

Aslin, R. N. & Shea, S. L. (1990). Velocity thresholds in human infants: implications for the perception of motion. *Developmental Psychology*, **26**, 589-598.

Atkinson, J. (1993). A neurobiological approach to the development of 'where' and 'what' systems for spatial representation in human infants. In Eilan, E., Brewer, B. & McCarthy, R. (Eds), *Problems in the Philosophy and Psychology of Spatial Representation.* Oxford: Blackwell (in press).

Atkinson, J. & Braddick, O. J. (1990). The developmental course of cortical processing streams in the human infant. In Blakemore, C. (Ed), *Vision: Coding and Efficiency.* Cambridge: Cambridge University Press.

Atkinson, J. & Braddick, O. J. (1981). Development of optokinetic nystagmus in infants: an indicator of cortical binocularity? In Fisher, D. F., Monty, R. A. & Senders, J. W. (Eds), *Eye movements: Cognition and visual perception.* Hillsdale, NJ: Erlbaum.

Atkinson, J. & Braddick, O. J. (1992). Visual segmentation of oriented textures by infants. *Behavioural Brain Research.* **49**, 123-131.

Atkinson, J., Braddick, O. J. & Moar, K. (1977). Development of contrast sensitivity over the first 3 months of life of the human infant. *Vision Research*, **17**, 1037-1044.

Atkinson, J., Hood, B., Wattam-Bell, J., Anker, S. & Tricklebank, J. (1988). Development of orientation discrimination in infancy. *Perception*, **17**, 587-595.

Baker, C. L. & Braddick, O. J. (1982a). Does segregation of differently moving areas depend on relative or absolute displacement? *Vision Research*, **22**, 851-856.

Baker, C. L. & Braddick, O. J. (1982b). The basis of area and dot number effects in random dot motion perception. *Vision Research*, **22**, 1253-1259.

Baker, C. L. & Braddick, O. J. (1985a). Eccentricity-dependent scaling of the limits for short-range apparent motion. *Vision Research*, **25**, 803-812.

Baker, C. L. & Braddick, O. J. (1985b). Temporal properties of the short-range process in apparent motion. *Perception*, **14**, 181-192.

Baker, C. L. & Cynader, M. S. (1986). Spatial receptive field properties of direction selective neurons in cat striate cortex. *Journal of Neurophysiology*, **55**, 1136-1152.

Banks, M. S. & Salapatek, P. (1978). Acuity and contrast sensitivity in 1-, 2- and 3-month-old human infants. *Investigative Ophthalmology and Visual Science*, **17**, 361-365.

Bradbury, A., Bertenthal, B. I. & Kramer, S. J. (1990). Minimum velocity thresholds in 12- and 20-week infants. *Investigative Ophthalmology and Visual Science (Suppl)*, **31**, 9.

Bonnet, C. (1982). Thresholds of visual motion. In Wertheim, A. H., Wagenaar, W. A. & Leibowitz, H. W. (Eds), *Tutorials on motion perception.* New York: Plenum.

Bracewell, R. N. (1986). *The Fourier Transform and its Applications*. New York: McGraw-Hill.

Braddick, O. J. (1974). A short-range process in apparent motion. *Vision Research*, **14**, 519-527.

Braddick, O. J. (1980). Low-level and high-level processes in apparent motion. *Philosophical Transactions of the Royal Society B*, **290**, 137-151.

Braddick, O. J. (1993a). Orientation- and motion-selective mechanisms in infants. In

Simons, K. (Ed), *Infant Vision: Basic and Clinical Research.* Committee on Vision, Commission on Behavioural and Social Sciences and Education, National Research Council. New York: Oxford University Press (in press).

Braddick, O. J. (1993b). Segmentation versus integration in visual motion processing. *Trends in Neuroscience*, (in press).

Braddick, O. J. & Atkinson, J. (1983). Some recent findings on the development of human binocularity: a review. *Behavioural Brain Research*, **10**, 141-150.

Braddick, O. J., Atkinson, J. & Campbell, F. W. (1978). Channels in vision: basic aspects. In Held, R., Leibowitz, H. & Teuber, H. L. (Eds), *Handbook of Sensory Physiology, Vol. VIII: Perception.* Oxford: Oxford University Press.

Braddick, O. J., Atkinson, J. & Wattam-Bell, J. (1986). Development of the discrimination of spatial phase in infancy. *Vision Research*, **26**, 1223-1239.

Braddick, O. J., Atkinson, J. & Wattam-Bell, J. (1989a). Development of visual cortical selectivity: binocularity, orientation and direction of motion. In von Euler, C., Forssberg, H. & Lagercrantz, H. (Eds.), *Neurobiology of Early Infant Behaviour* (pp. 165-172). Wenner-Gren International Symposium Series, Vol. 55. London: Macmillan.

Braddick, O. J., Atkinson, J., Wattam-Bell, J. & Hood, B. (1989b). Characteristics of orientation-selective mechanisms in early infancy. *Investigative Ophthalmology and Visual Science (Suppl)*, **30**, 313.

Burr, D. C., Ross, J. & Morrone, M. C. (1986). Seeing objects in motion. *Proceedings of the Royal Society* B, **227**, 249-265.

Chang, J. J. & Julesz, B. (1983a). Displacement limits, directional anisotropy and direction versus form discrimination in random dot cinematograms. *Vision Research*, **23**, 639-646.

Chang, J. J. & Julesz, B. (1983b). Displacement limits for spatial-frequency filtered random-dot cinematograms in apparent motion. *Vision Research*, **23**, 1379-1385.

Chang, J. J. & Julesz, B. (1984). Cooperative phenomena in apparent movement perception of random dot cinematograms. *Vision Research*, **24**, 1781-1788.

Chubb, C. & Sperling, G. (1988). Drift-balanced random stimuli: a general basis for studying non-Fourier motion perception. *Journal of the Optical Society of America*, **A5**, 1986-2007.

Cleary, R. & Braddick, O. J. (1990a). Direction discrimination for band-pass filtered random dot kinematograms. *Vision Research*, **30**, 303-316.

Cleary, R. & Braddick, O. J. (1990b). Masking of low frequency information in short-range apparent motion. *Vision Research*, **30**, 317-327.

Dannemiller, J. L. & Freedland, R. L. (1989). The detection of slow stimulus movement in 2-5-month-olds. *Journal of Experimental Child Psychology*, **47**, 337-355.

Dannemiller, J. L. & Freedland, R. L. (1991). Detection of standing wave motion by human infants. *Investigative Ophthalmology and Visual Science (Suppl)*, **32**, 1044.

Dannemiller, J. L. (1992). Speed determines infants' detection of standing wave motion. *Investigative Ophthalmology and Visual Science (Suppl)*, **33**, 714.

Daw, N. W. & Wyatt, H. J. (1976). Kittens reared in a unidirectional environment: evidence for a critical period. *Journal of Physiology*, **257**, 155-170.

Derrington, A. M. & Lennie, P. (1984). Spatial and temporal contrast sensitivities of neurones in the lateral geniculate nucleus of the macaque. *Journal of Physiology*, **357**, 219-240.

DeValois, R. L., Yund, E. W. & Helper, N. (1982a). The orientation and direction selectivity of cells in the macaque visual cortex. *Vision Research*, **22**, 531-544.

DeValois, R. L., Albrecht, D. G. & Thorell, L. G. (1982b). Spatial frequency selectivity of cells in the macaque visual cortex. *Vision Research*, **22**, 545-559.

De Yoe, E. A. & Van Essen, D. C. (1988). Concurrent processing streams in monkey visual cortex. *Trends in Neuroscience*, **11**, 219-226.

Durbin, R. & Mitchison, G. (1990). A dimension reduction framework for understanding cortical maps. *Nature*, **343**, 644-647.

Eagle, R. A. (1992). Spatial characteristics of human visual motion processing. DPhil Thesis, University of Oxford.

Gibson, J. J. (1966). *The Senses Considered as Perceptual Systems*. Boston: Houghton-Mifflin.

Gibson, E. J., Owsley, C. J., Walker, A. & Megaw-Nice, J. (1979). Development of the perception of invariants: substance and shape. *Perception*, **8**, 609-619.

Gwiazda, J., Brill, S., Mohindra, I. & Held R. (1980). Preferential looking acuity in

infants from two to fifty-eight weeks of age. *American Journal of Optometry and Physiological Optics*, **57**, 428-432.

Hartmann, E. E. & Banks, M. S. (1992). Temporal contrast sensitivity in human infants. *Vision Research*, **32**, 1163-1168.

Hoffmann, K. P. (1986). Visual inputs relevant for optokinetic nystagmus in mammals. *Progress in Brain Research*, **64**, 75-84.

Hood, B., Atkinson, J., Braddick, O. J. & Wattam-Bell, J. (1992). Orientation selectivity in infancy: behavioural evidence for temporal sensitivity. *Perception*, **21**, 351-354.

Horowitz, F. D. (1975). Infant attention and discrimination: methodological and substantive issues. *Monographs of the Society for Research on Child Development*, **39**, (5-6, serial no. 158), 1-15.

Horridge, G. A. (1984). The evolution of visual processing and the construction of seeing systems. *Proceedings of the Royal Society* B, **230**, 279-292.

Hubel, D. H. & Weisel, T. N. (1959). Receptive fields of single neurons in the cat's striate cortex. *Journal of Physiology*, **148**, 574-591.

Huttenlocher, P. R. & de Courten, C. (1987). The development of synapses in striate cortex of man. *Human Neurobiology*, **6**, 1-9.

Kaufmann, F., Stucki, M. & Kaufmann-Hayoz, R. (1985). Development of infants' sensitivity for slow and rapid motions. *Infant Behaviour and Development*, **8**, 89-95.

Kellmann, P. J. & Spelke, E. S. (1983). Perception of partly occluded objects in infancy. *Cognitive Psychology*, **15**, 483-524.

Kramer, S. J. & Bertenthal, B. I. (1989). Infants' sensitivity to motion in random-dot kinematograms. *Investigative Ophthalmology and Visual Science (Suppl.)*, **30**, 312.

Kremenitzer, J. P., Vaughan, H. G., Kurtzberg, D. & Dowling, K. (1979). Smooth-pursuit eye movements in the newborn infant. *Child Development*, **50**, 442-448.

Lehky, S. R. (1985). Temporal properties of visual channels measured by masking. *Journal of the Optical Society of America*, **2**, 1260-1272.

Lisberger, S. G., Morris, E. J. & Tychsen, L. (1987). Visual motion processing and sensory-motor integration for smooth pursuit eye movements. *Annual Review of Neuroscience*, **10**, 97-129.

Maunsell, J. H. R. & Newsome, W. T. (1987). Visual processing in monkey extrastriate cortex. *Annual Review of Neuroscience*, **10**, 363-401.

McKee, S. P. & Welch, L. (1985). Sequential recruitment in the discrimination of velocity. *Journal of the Optical Society of America A*, **2**, 243-251.

Mikami, A., Newsome, W. T. & Wurtz, R. H. (1986). Motion selectivity in macaque visual cortex. II. Spatiotemporal range of directional interactions in MT and V1. *Journal of Neurophysiology*, **55**, 1328-1351.

Mishkin, M., Ungerleider, L. G. & Macko, K. A. (1983). Object vision and spatial vision: two cortical pathways. *Trends in Neuroscience*, **6**, 414-417.

Mohn, G. (1989). The development of binocular and monocular optokinetic nystagmus in human infants. *Investigative Ophthalmology and Visual Science (Suppl.)*, **40**, 49.

Morgan, M. J. (1992). Spatial filtering precedes motion detection. *Nature*, **355**, 344-346.

Moskowitz, A. & Sokol, S. (1980). Spatial and temporal interaction of pattern-evoked cortical potentials in human infants. *Vision Research*, **20**, 699-708.

Naegele, J. R. & Held, R. (1982). The postnatal development of monocular optokinetic nystagmus in infants. *Vision Research*, **22**, 341-346.

Nakayama, K. (1985). Biological image motion processing: a review. *Vision Research*, **25**, 625-660.

Nakayama, K. & Silverman, G. H. (1984). Temporal and spatial characteristics of the upper displacement limit for motion in random dots. *Vision Research*, **24**, 293-299.

Nawrot, M. & Sekuler, R. (1990). Assimilation and contrast effects in motion detection. *Vision Research*, **30**, 1439-1451.

Newsome, W. T., Mikami, A. & Wurtz, R. H. (1986). Motion selectivity in macaque visual cortex. III. Psychophysics and physiology of apparent motion. *Journal of Neurophysiology*, **55**, 1340-1351.

Newsome, W. T. & Pare, E. B. (1988). A selective impairment of motion processing following lesions of the middle temporal visual area (MT). *Journal of Neuroscience*, **8**, 2201-2211.

Norcia, A. M., Garcia, H., Humphrey, R., Holmes, A. & Orel-Bixler, D. (1991). Anomolous motion VEPs in infants and in infantile esotropia. *Investigative*

Ophthalmology and Visual Science, **32**, 436-439.

Obermayer, K., Ritter, H. & Schulten, K. (1990). A principle for the formation of the spatial structure of cortical feature maps. *Proceedings of the National Academy of Science*, **87**, 8345-8349.

Orban, G. A., Kennedy, H. & Bullier, J. (1986). Velocity sensitivity and direction selectivity in areas V1 and V2 of the monkey: Influence of eccentricity. *Journal of Neurophysiology*, **56**, 462-480.

Price, D. J., Zumbroich, T. J. & Blakemore, C. (1988). Development of stimulus selectivity and functional organisation in the suprasylvian visual cortex of the cat. *Proceedings of the Royal Society B*, **223**, 123-163.

Regal, D. M. (1981). Development of critical flicker frequency in human infants. *Vision Research*, **21**, 549-555.

Reichardt, W. (1961). Autocorrelation, a principle for the evaluation of sensory information by the central nervous system. In Rosenbluth, W. A. (Ed), *Sensory Communication* (pp 303-317). Cambridge: MIT Press.

Shea, S. L. & Aslin, R. N. (1990). Oculomotor responses to step-ramp targets by young human infants. *Vision Research*, **30**, 1077-1092.

Sireteanu, R. & Rieth, C. (1992a). Texture segregation in infants and children. *Behavioural Brain Research*, **49**, 133-139.

Sireteanu, R. & Rieth, C. (1992b). Texture segmentation based on line orientation: an infant study with habituation/novelty preference. *Perception*, **21**, A3.

Slater, A. (1992). Paper presented at the British Infancy Research Group meeting, Exeter, July 1992.

Slater, A., Morison, V., Town, C. & Rose, D. (1985). Movement perception and identity constancy in the new-born baby. *British Journal of Developmental Psychology*, **3**, 211-220.

Slater, A., Morison, V. & Somers, M. (1988). Orientation discrimination and cortical function in the human newborn. *Perception*, **17**, 597-602.

Smith, J. C. (1989). Development of binocular vision in normal and strabismic infants. PhD Thesis, Cambridge University.

Smith, J. C., Atkinson, J., Anker, S. & Moore, A. T. (1991). A prospective study of

binocularity and amblyopia in strabismic infants before and after corrective surgery: implications for the human critical period. *Clinical Vision Science*, **6**, 335-353.

Snowden, R. J. (1989). Motions in orthogonal directions are mutually suppressive. *Journal of the Optical Society of America A*, **6**, 1096-1101.

Snowden, R. J. & Braddick, O. J. (1989a). The combination of motion signal over time. *Vision Research*, **29**, 1621-1630.

Snowden, R. J. & Braddick, O. J. (1989b). Extension of displacement limits in multiple-exposure sequences of apparent motion. *Vision Research*, **29**, 1777-1788.

Snowden, R. J. & Braddick, O. J. (1990). Differences in the processing of short-range apparent motion at small and large displacements. *Vision Research*, **30**, 1211-1222.

Spitz, R. V. & Kleffner D. (1991). Element size influences infant perception of local, not global motion. Paper presented at the 1991 Biennial Meeting of the Society for Research in Child Development, Seattle, Washington.

Spitz, R. V., Stiles, J. & Siegel, R. M. (1992). Infant use of relative motion as information for form: evidence of spatio-temporal integration of complex motion displays. *Perception and Psychophysics*, (in press).

Stephens. B. R. & Banks, M. S. (1987). Contrast discrimination in human infants. *Journal of Experimental Psychology: Human Perception and Performance*, **13**, 558-565.

Swanson, W. H. & Birch, E. E. (1990). Infant spatiotemporal vision: Dependence of spatial contrast sensitivity on temporal frequency. *Vision Research*, **30**, 1033-1048.

Swindale, N. V. (1982). A model for the formation of orientation columns. *Proceedings of the Royal Society B*, **215**, 211-230.

Swindale, N. V., Matsubara, J. A. & Cynader, M. S. (1987). Surface organisation of orientation and direction selectivity in cat area 18. *Journal of Neuroscience*, **7**, 1414-1427.

Teller, D. Y. (1979). The forced-choice preferential looking procedure: A psychophysical technique for use with human infants. *Infant Behavior and Development*, **2**, 135-153.

Teller, D. Y., Lindsey, D. T., Mar, C. M., Succop, A. & Mahal, M. R. (1992). Infant temporal contrast sensitivity at low temporal frequencies. *Vision Research*, **32**, 1157-

1162.

Tychsen, L. (1989). Primary maldevelopment of visual motion pathway in humans. *Investigative Ophthalmology and Visual Science (Suppl)*, **30**, 302.

Tychsen, L. & Lisberger, S. G. (1986). Maldevelopment of visual motion processing in humans who had strabismus with onset in infancy. *Journal of Neuroscience*, **6**, 2495-2508.

Van Doorn, A. J. & Koendrink, J. J. (1982a). Temporal properties of the visual detectability of moving spatial white noise. *Experimental Brain Research*, **45**, 179-188.

Van Doorn, A. J. & Koendrink, J. J. (1982b). Spatial properties of the visual detectability of moving spatial white noise. *Experimental Brain Research*, **45**, 189-195.

Van Doorn, A. J. & Koendrink, J. J. (1984). Spatiotemporal integration in the detectability of motion. *Vision Research*, **24**, 47-53.

Van de Grind, W. A., van Doorn, J. A. & Koendrink, J. J. (1983). Detection of coherent movement in peripherally viewed random-dot patterns. *Journal of the Optical Society of America*, **73**, 1674-1683.

Van de Grind, W. A. Koendrink, J. J. & van Doorn, A. J. (1986). The distribution of human motion detector properties in the monocular visual field. *Vision Research*, **26**, 797-810.

Van Santen, J. P. H. & Sperling, G. (1985). Elaborated Reichardt detectors. *Journal of the Optical Society of America*, **A2**, 300-321.

Van Sluyters, R. C., Atkinson, J., Banks, M. S., Held, R. M., Hoffmann, K. P. & Shatz, C. J. (1990). The development of vision and visual perception. In Spillman, L. & Werner, J. S. (Eds), *Visual Perception: The Neurophysiological Foundations* (pp. 349-379). San Diego: Academic Press.

Volkmann, F. C. & Dobson, V. (1976). Infant responses of ocular fixation to moving visual stimuli. *Journal of Experimental Child Psychology*, **22**, 86-99.

Watson, A. B. & Ahumada, A. J. (1985). Model of human visual-motion sensing. *Journal of the Optical Society of America A*, **2**, 322-341.

Watson, A. B. & Robson, J. G. (1981). Discrimination at threshold: labelled detectors

in human vision. *Vision Research*, **21**, 1115-1122.

Watson, A. B., Thompson, P. G., Murphy, B. J. & Nachmias, J. (1980). Summation and discrimination of gratings moving in opposite directions. *Vision Research*, **20**, 341-347.

Wattam-Bell, J. (1991a). Development of motion-specific cortical responses in infancy. *Vision Research*, **31**, 287-297.

Wattam-Bell, J. (1991b). Displacement limits for the discrimination of motion direction in infancy. *Investigative Ophthalmology and Visual Science (Suppl.)*, **32**, 964.

Wattam-Bell, J. (1992a). The development of maximum displacement limits for the discrimination of motion direction in infancy. *Vision Research*, **32**, 621-630.

Wattam-Bell, J. (1992b). Are one-month-old infants motion-blind? *Perception*, **21**, A2.

Wattam-Bell, J. (1993). One-month-old infants fail in a motion direction discrimination task. *Investigative Ophthalmology and Visual Science (Suppl.)*, **34**, 1356.

Wattam-Bell, J., Braddick, O. J., Atkinson, J. & Day, J. (1987). Measures of infant binocularity in a group at risk of strabismus. *Clinical Vision Sciences*, **1**, 327-336.

Wetherill, G. B. & Levitt H. (1965). Sequential estimation of points on a psychometric function. *British Journal of Mathematical and Statistical Psychology*, **18**, 1-10.

Williams, D. W. & Sekuler, R. (1984). Coherent global motion percepts from stochastic local motions. *Vision Research*, **24**, 55-62.

Williams, D. W., Phillips, G. & Sekuler, R. (1986). Hysteresis in the perception of motion direction as evidence of neural cooperativity. *Nature*, **324**, 253-255.

Wilson, H. R. (1988). Development of spatiotemporal mechanisms in infant vision. *Vision Research*, **28**, 611-628.

Wilson, H. R., Levi, D., Maffei, L., Rovamo, J. & DeValois, R. (1991). The perception of form: Retina to striate cortex. In Spillman, L. & Werner, L. S. (Eds), *Visual Perception: The Neurophysiological Foundations* (pp. 231-272). San Diego: Academic Press.

Yonas, A. & Granrud, C. E. (1985). The development of sensitivity to kinetic, binocular and pictorial depth information in human infants. In Ingle, D. J., Jeannerod, M. & Lee, D. N. (Eds), *Brain Mechanisms and Spatial Vision*. Dordrecht: Martinus Nijhoff.